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REVIEW ARTICLE

Management of abiotic stresses by microbiome-based engineering of the rhizosphere

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Abstract

Abiotic stresses detrimentally affect both plant and soil health, threatening food security in an ever-increasing world population. Sustainable agriculture is necessary to augment crop yield with simultaneous management of stresses. Limitations of conventional bioinoculants have shifted the focus to more effective alternatives. With the realization of the potential of rhizospheric microbiome engineering in enhancing plant's fitness under stress, efforts have accelerated in this direction. Though still in its infancy, microbiome-based engineering has gained popularity because of its advantages over the microbe-based approach. This review briefly presents major abiotic stresses afflicting arable land, followed by an introduction to the conventional approach of microbe-based enhancement of plant attributes and stress mitigation with its inherent limitations. It then focuses on the significance of the rhizospheric microbiome and possibilities of harnessing its potential by its strategic engineering for stress management. Further, success stories related to two major approaches of microbiome engineering (generation of synthetic microbial community/consortium, and host-mediated artificial selection) pertaining to stress management have been critically presented. Together with bringing forth the challenges associated with the wide application of rhizospheric microbiome engineering in agriculture, the review proposes the adoption of a combinational scheme for the same, bringing together ecological and reductionist approaches for improvised sustainable agricultural practices.

KEYWORDS
bioinoculant, host-mediated artificial selection, stress mitigation, sustainable agriculture, synthetic microbial community

INTRODUCTION

According to United Nations (2019), the global population is expected to reach 9.7 billion in 2050 from the present population of 7.7 billion. Around 9.2% of the total world population is experiencing food insecurity (FAO, 2021). For catering to the growing demands of a rapidly increasing human population, approx. 70% increase in overall crop productivity is required (Ke et al., 2021). The green revolution had positively impacted crop yield through the intensive use of agrochemicals and genetically modified crops. However, it resulted in the adoption

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Rashi Tyagi and Salila Pradhan Equal contribution of unsustainable practices, which eventually adversely affected soil health. Application of chemical fertilizers, growth regulators, and pesticides are not encouraged for long-term agricultural practices as they cause soil degradation (Tallapragada & Seshagiri, 2017). It is reported that 90% of the applied chemical pesticides are lost through leaching, photolysis, volatilization and run-off during the application, whilst only a minor fraction reach their targets (Liang et al., 2017). Many major crops like wheat, maize, and rice have encountered low productivity with the progression of time (Ray et al., 2012). Thus, we need novel and efficient agricultural practices that can ensure high crop yield in an economical and eco-friendly manner (Hussain et al., 2018). Sustainable agriculture deals with various practices that do not compromise with crop productivity and environmental balance (Kumar et al., 2019). The application of organic inputs in farming is one of the best examples of ensuring sustainable crop yield (Rajput et al., 2019). Amendment with biostimulants (including chemicals and microorganisms) is a promising tool, and has been critically reviewed recently (de Vasconcelos & Chaves, 2019; Shahrajabian et al., 2021).

As the microbes present in soil and rhizospheres of plants are pivotal for the maintenance of environmental homeostasis (Barea, 2015), they are considered one of the best alternatives to chemical fertilizers (Kumawat et al., 2021). However, the inherent limitations associated with the application of plant growth-promoting and biocontrol microbes have emphasized the need to look for further strategies that are robust. Sustainable agriculture can be brought about by harnessing the benefits of microbiome-based rhizospheric engineering approach, facilitating crop improvement, and ensuring abiotic and biotic stress management (Ahkami et al., 2017; Arif et al., 2020; Hakim et al., 2021; Kaul et al., 2021; Ke et al., 2021). In this review, the major abiotic stress constraints to enhance agricultural productivity have been presented briefly. In addition, the application of microbiome-based rhizospheric engineering, and its advantages over microbe-based application on plants under stress conditions have also been critically discussed.

ABIOTIC STRESSES AFFECTING AGRICULTURAL SYSTEMS

Stress factors are major deterrents in the agricultural systems, adversely affecting plant growth and development, and eventually hindering crop productivity (Carmen & Roberto, 2011). Abiotic stresses include drought, edaphic factors, submergence (floods), extreme temperatures, and radiations. Edaphic factors majorly include chemical factors like nutrient deficiency, salinity, alkalinity, low pH, low redox, presence of contaminants in soil, as well as physical factors like susceptibility to erosion, low water holding capacity, structural instability, etc. (Minhas, 2017).

Abiotic stresses have impacted agriculture worldwide. On a global scale, drought has been reported to have the maximum impact (64%) on the global land area, followed by cold (57%), acidic soils (15%), submergence due to flood (13%), mineral deficiency, low fertility (9%), and salinity stress (6%) (Cramer et al., 2011). These stresses limit the crop production on about 1.4 billion ha of cultivated land globally (Venkateswarlu & Prasad, 2012). Further, the use of chemical pesticides seriously impacts the environment and human health. Common problems encountered are soil infertility, lethal effects on plant-beneficial microbes, eutrophication of water body and groundwater pollution due to leaching (Arif et al., 2020). The major abiotic stresses that impact agricultural productivity have been discussed below.

Several factors such as reduced precipitation and increased evaporation, besides soil conditions, contribute to drought (Gornall et al., 2010). Drought conditions lead to the decreased water potential of leaves and stomatal opening, decrement in leaf size, reduced number and size of seeds, hindered seedling establishment, retarded growth of roots, etc. (Osakabe et al., 2014; Xu et al., 2016). Drought also enhances the biosynthesis of ethylene, which leads to premature leaf senescence (Meena et al., 2017).

In agricultural soils, salinity refers to the accumulation of salt at levels that can sufficiently reduce the growth and productivity of crops. Salinity is either caused due to poor quality of irrigated water or excessive concentration of salts naturally present in soil due to weathering of minerals (Bhardwaj & Kumar, 2020). Salinity stress persisting for longer durations can also cause oxidative damage leading to the generation of reactive oxygen species (ROS), which are destructive to plant proteins, membrane lipids and nucleic acids (Álvarez & Sánchez-Blanco, 2014; Sánchez-Rodríguez et al., 2010).

Acidification of soil occurs due to the chemical decomposition of the parent material of soil, oxidative weathering, organic matter decay, excessive use of fertilizers, acid rains, etc. The pH of acidic soil is below 5.5; the acidic nature of soil leads to severe losses in crop productivity, due to low saturation of base, excess concentration of aluminium, iron, and manganese, deficiency of micronutrients, poor water retention capacity, besides poor availability of nitrogen and phosphorus (Minhas, 2017).

High temperature leads to denaturation of proteins resulting in the inactivation of enzymes and disruption of structural proteins (Wahid et al., 2007), whilst at low temperatures (0–15°C), chilling alters the integrity of the cell membrane. Temperature below 0°C causes injury to plant cells due to the formation of ice crystals (Chinnappa et al., 2017). Temperature stress severely impacts photosynthesis and seed germination, and can also induce oxidative stress, eventually leading to compromised plant growth and crop productivity (Hasanuzzaman et al., 2013).

The deficiency of even a single nutrient interferes with the expression of other nutrients leading to decreased fitness and health of plants, which further lowers crop productivity (Minhas, 2017). Contrarily, nutrient toxicity is caused due to the presence of an excess of any given nutrient, e.g., frequent application of a large amount of fertilizers. Multiple nutrient deficiencies occur due to continued low input agriculture and high intensity of cropping that does not provide adequate time for nutrient replenishment in soil (Sharma & Singh, 2012); nutrient deficiency has been more frequently witnessed in agricultural systems as compared to nutrient toxicity (Barker & Pilbeam, 2015).

Using chemical pesticides in agricultural sites, besides direct dumping of industrial wastes in nearby sites, leads to the accumulation of heavy metals beyond toxicity limits (Chibuike & Obiora, 2014). The elevated concentrations of heavy metals in soil accelerate the mortality of plants by inducing oxidative stress, inhibition of essential plant cytoplasmic enzymes required for plant metabolism, and indirect substitution of essential nutrients (Assche & Clijsters, 1990). Crops grown in contaminated soil accumulate heavy metals in edible parts. The consumption of these contaminated edible parts leads to the migration of heavy metals in the food chain causing a serious threat to human life as well as the ecosystem (Shukla et al., 2017).

APPLICATION OF BIOINOCULANTS TO MITIGATE ABIOTIC STRESSES: THE CONVENTIONAL APPROACH

Plants exist in nature along with a plethora of microbes inhabiting different plant parts (Turner et al., 2013). The application of microorganisms in agricultural systems for stress mitigation has been in practice for a long time. This is based on using bioinoculants in the form of biofertilizers, biopesticides, bioherbicides and bio-control agents (Ahirwar et al., 2019). Bioinoculants represent beneficial microbes that enhance plant growth and development, in addition to enhancing crop productivity, and help plants in combating different stresses (Chaudhary et al., 2020). Bioinoculants can be applied as a single microbial strain or as consortia of selected microbial strains (Compant et al., 2019). Bioinoculants are mostly applied to the rhizospheric region of plants, directly or indirectly through seeds (Jambhulkar et al., 2016).

The contribution of plant associated microbiome in enhancing agricultural crop productivity under abiotic stresses has been widely studied. Plant growth-promoting microorganisms (PGPM) have been reported to play crucial roles in the mitigation of drought stress by different mechanisms like increasing cytokinin levels (Liu et al., 2019), elevating auxin and abscisic acid (ABA) levels (Liu et al., 2013), and also by enhancing gibberellic acid in plants (Ahkami et al., 2017; Kang et al., 2014). PGPM have also been reported to mitigate salinity stress by modifying plant's physiology, regulating various hormonal cross-talks, and impacting plant development (Kumar et al., 2019; Ramadoss et al., 2013). For example, inoculation with arbuscular mycorrhizal fungi (AMF) was effective in the management of salinity stress in lettuce (Santander et al., 2019). Another effective microbe, *Pseudomonas frederiksbergensis* OS261, has been reported to contribute to the mitigation of salinity stress in red pepper by lowering ethylene emission and regulating the production of antioxidant enzymes (Chatterjee et al., 2017).

Despite the promising roles of bioinoculants in bringing about betterment in agriculture, their efficacy is limited (Dubey & Sharma, 2019). The main reasons for the limited potential of bioinoculants are reduced persistence and survivability of introduced microbes in fields (Egamberdieva & Lugtenberg, 2014; Orozco-Mosqueda et al., 2021; Mitter et al., 2021), though there have been some success stories in enhancing their survivability and efficacy by supplementing with metabolites like extracellular polymeric substances (Tewari & Sharma, 2020a, 2020b). A prominent effect of bioinoculants on plants has been observed at early growth stages, whilst at a later stage, it declines (Sharma et al., 2017). A prime reason could be the failure of introduced bioinoculants to colonize the plant's rhizosphere, with indigenous microbes outcompeting them (Dubey & Sharma, 2019). The selection pressure imposed by the plant for microbe colonization plays a crucial role in governing the survival and activity of bioinoculants. Plants select specific microbial communities by producing root exudates and triggering host immune responses, which poses a risk to the survival of bioinoculants in its vicinity (Marasco et al., 2012). Also, it is challenging to track the bioinoculants post their application, although attempts have been made towards developing methods for monitoring bioinoculants in soil (Manfredini et al., 2021). The crop yield has been reported to be inconsistent or moderate upon application of bioinoculant strains, and in general, the population of bioinoculant strains in soil has been reported to decline gradually (Scagliola et al., 2021; Sharma et al., 2017, 2020). Besides this, type of farming practice also plays an important role in governing the fate or efficacy of action of bioinoculants. Traditional ways of mitigating salinity stress are based on the application of chemical amendments and organic inputs, and bringing changes in agricultural land through modifying drainage and irrigation systems (Mohanavelu et al., 2021). Some farmers apply a heavy dosage of agrochemicals in bioinoculant-applied soil, which negatively affects the introduced microbes by disturbing the composition and abundance of indigenous microbes, and soil pH (Qiu et al., 2019).

The challenges related to conventional approaches of bioinoculant applications limit their use. It has been shown that single microbe inoculants have been less effective in action as compared to a combination of microbes in different plant systems (Bradáčová et al., 2019; Nosheen et al., 2021; Sharma et al., 2017, 2020). The success of application of multiple bioinoculants depends upon their synergistic interactions, and their better adaptability to counteract environmental constraints as compared to single bioinoculants (Bradáčová et al., 2019). Hence, in recent times, the focus is rapidly shifting towards the application of microbiome as a whole, for sustainable agriculture. The main advantage of preferring the microbiome over microbial bioinoculants is their greater chances of survival since they are already adapted to the plants' environment, resulting in no or less competition from resident microflora (Orozco-Mosqueda et al., 2018). Thus, the emerging era of microbiome-mediated approaches is likely to bypass the limitations encountered with the application of microbial inoculants.

HARNESSING THE MICROBIOME OF PLANTS

The multicellular eukaryotic organisms together with their associated microbial components have been referred to as 'holobiont' (Hartmann et al., 2019). In plants, the microbial population includes archaea, bacteria, fungi, protozoa, and viruses. These are acquired by vertical transmission from the host plant to its offspring via seeds and/or by horizontal transmission from the soil environment (Saikkonen et al., 2020). The complex interactions between plants and microbial populations exist predominantly in the rhizosphere, which represents one of the most complex systems because of 10-fold higher richness of actinobacteria, copiotrophs, oligotrophs and pseudomonads in comparison to bulk soil (Donn et al., 2015). The rhizosphere is also considered a highly responsive and dynamic system compared to the bulk soil (Compant et al., 2019; Donn et al., 2015). The production of root exudates such as amino acids, plant growth regulators, fatty acids, nucleotides, vitamins, organic acids, etc. has been reported to be crucial in governing the microbial diversity in the rhizospheric soil (Hartmann et al., 2008; Mendes et al., 2013). The associated microbial population is referred to as 'second genome' of the plant because of their significant contributions to affecting the essential life traits of the host plant and determining its overall fitness (Compant et al., 2019). As discussed earlier, the plant associated microbial communities, especially the rhizospheric microbial communities, can aid in plant growth promotion, bringing about crop protection and improvement in plant nutrition under the influence of abiotic and biotic stress factors (Ahirwar et al., 2019). Thus, understanding the complexity, followed by manipulating the composition of the root microbiome, can be utilized for diagnostic and therapeutic purposes in plants. Consequently, this can help in mitigating stresses in an efficient manner and enable the promotion of plant growth and enhancement of the crop yield.

Despite the existing knowledge about the role of microbes in mediating the overall well-being of plants, the potential to harness the plant's microbiome is limited due to the constraints of culturing techniques, as only 5–10% of the rhizospheric microbes are culturable (Turner et al., 2013). However, the recent advancements in "omics" approaches, qPCR and non-PCR-based methods, community amplicon sequencing, etc. allow researchers to unravel the diversity of the microbiome and understand the complex interactions existing between microbe-microbe and plant-microbe (Ijaz et al., 2021; Xu, Pierroz, et al., 2021). Further, these studies can be utilized to engineer the rhizospheric microbiome as mediated by the host or for designing multispecies "synthetic" microbial communities/consortia, which can mitigate various stresses and/or promote plant growth (Saikkonen et al., 2020).

Rhizospheric microbiome engineering as a promising tool for stress mitigation in plants

The rhizosphere is a hub harbouring several beneficial microorganisms for plants. Environmental perturbations dynamically modulate the rhizospheric microbial community structure in plants. Thus, strategic management of the rhizospheric microbiome of plants can serve as a key to stress mitigation and disease management (Sarker et al., 2021). A plethora of factors, viz. soil physicochemical properties like pH, temperature etc., environmental perturbations like drought, and salinity, plant genotype as well as diverse agricultural practices have a substantial impact on shaping the rhizospheric microbial community structure (Abdul Rahman et al., 2021). Numerous microbes residing in the rhizospheric soil thrive together via intricate networks, and can exert a positive, neutral or negative influence on the holobiont (Babalola et al., 2021).

Many microbial members among them, play significant roles in alleviating detrimental effects of stress conditions in plants. The untapped potential of complex interactions existing between microbe-microbe and microbe-plant can be harnessed for stress mitigation in diverse agroecosystems, which can thereby lead to minimal use of chemicals and promotion of sustainable agriculture (Abdul Rahman et al., 2021; Hunter, 2016).

Engineering the rhizospheric microbiome can be mediated in different ways, viz. plant-based, metaorganism-based and microbiome-based approaches (Figure 1). Optimal utilization of these strategies include plant-based and metaorganism-based practices like plant breeding, crop rotation as well as microbiome engineering in a targeted manner, which can lead to efficient manipulation of the rhizospheric microbiome, resulting in crop improvement and amelioration of stresses (Arif et al., 2020; Harman et al., 2021; Kumar & Dubey, 2020; Quiza et al., 2015; Tosi et al., 2020).

Plant-based approach for rhizospheric engineering predominantly involves plant breeding methods and selection of appropriate cultivars, which promote the production of exudates, either stimulatory or inhibitory factors that favour the prevalence of selected microbial members in the rhizospheric community (Hartmann et al., 2009). Additionally, genetic modification of plants for enhancing the production of exudates or signalling molecules, generating mutants or transgenics exhibiting disease resistance due to the production of antagonistic molecules, transgenics producing quorum sensing signalling molecules or enzymes degrading them, also impact the rhizospheric microbial communities (Bakker et al., 2012; Koyama et al., 2000; Lynch et al., 2004; Zhang et al., 2015).

The metaorganism-based approach involves co-engineering of plants as well as the associated microbial communities for facilitating a particular metabolic pathway. For example, the plants engineered to produce opines were coinoculated with opine-degrading bacteria, leading to a trophic link based on the plant-bacterial interactions (Dessaux et al., 1998; Savka et al., 2002). Manipulation of the rhizospheric microbiome can also be mediated by supplementing fields with organic fertilizers that would increase soil organic carbon content and induce disease suppressiveness in soil (Mazzola, 2007). Particularly, organic amendments possess immense potential in maintaining soil fertility as well as soil microbial diversity (Bamdad et al., 2021; Scotti et al., 2015). There are reports which correlate organic farming practices with increased microbial diversity, but in-depth studies are needed to substantiate this observation and decipher

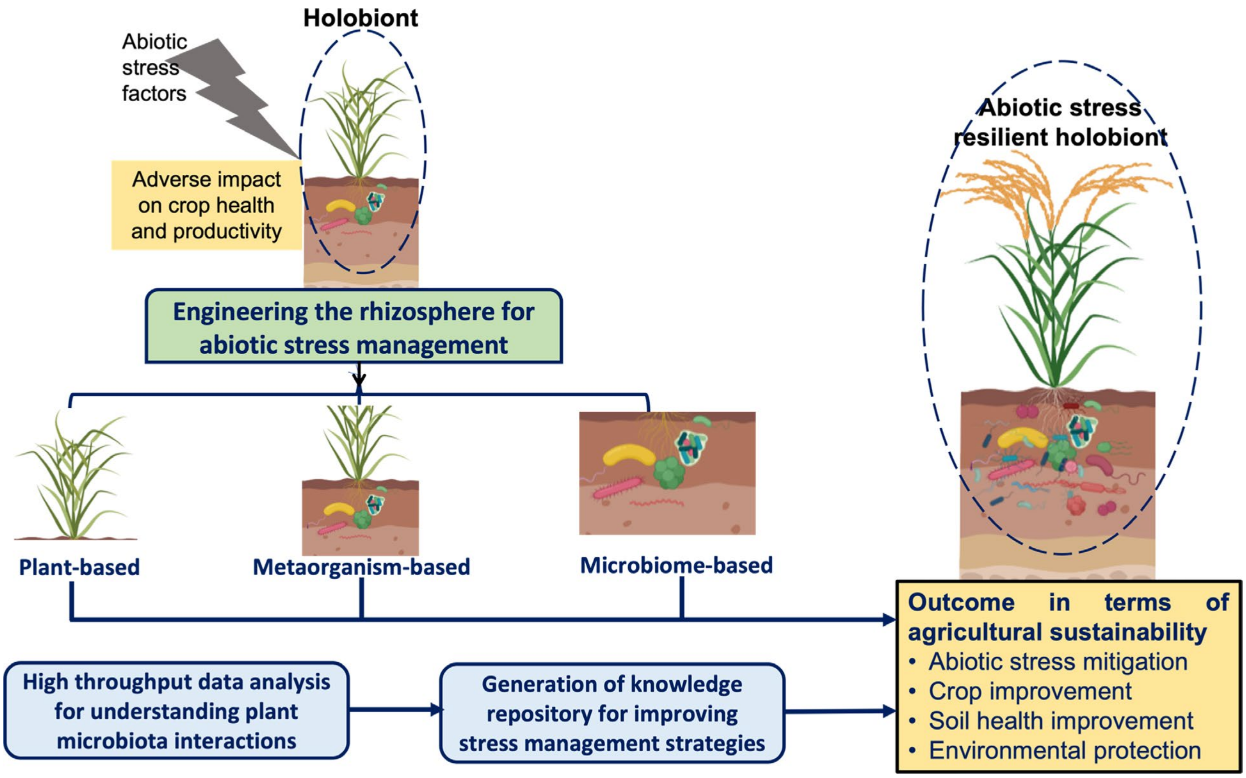

FIGURE 1 Abiotic stress mitigation in plants via rhizospheric engineering approaches. Eco-friendly stress management can be mediated by various strategies of rhizospheric engineering (plant-based, metaorganism-based and microbiome-based). Simultaneous utilization of advanced high-throughput technologies to generate knowledge repositories offering insights into plant-microbiome interactions can help in improvization of stress management strategies for ushering sustainability in agriculture (created using BioRender)

the mechanisms which shape the interactions between plant–soil-microbiota (Khatri & Sharma, 2021). In fact, organic amendments in combination with inorganic amendments and/PGPM have been reported to mediate salinity stress tolerance in plants (Alnahhas et al., 2020; Bello et al., 2021). Notably, agri-management practices affect the crop microbiomes either positively or negatively. Crop rotation has also been considered as a suitable practice for managing soil microbial diversity by making an appropriate choice of cultivation of crops and associated microbiomes, which can improve soil health and also induce disease suppressiveness in soil (Ryan et al., 2009). Recently, a study reported the significance of paddy-upland rotation in enriching microbial diversity of soil as well as diversifying the structure of microbiome, which is vital for improving soil health and agricultural sustainability (Hou et al., 2018). Thus, the need of the hour is to customize potent strategies to overcome environmental hurdles and achieve precise microbiome management by adopting best practices for diverse farming systems, paving way for sustainable agriculture (French et al., 2021).

There are several reports which demonstrate that microbe-mediated abiotic stress mitigation occurs through a range of mechanisms in plant systems. Studies based on multiomics approaches have resulted in an improved understanding of plant-microbe interactions, thus enabling advancements in microbe-mediated stress management (Inbaraj, 2021; Khan et al., 2021; Kumar et al., 2020; Mathur & Roy, 2021; Meena et al., 2017). However, similar progress is yet to be made in the arena of microbiome-mediated rhizospheric engineering. Microbiome-based rhizospheric engineering has emerged as a promising tool for addressing agricultural problems like management of plant diseases and low crop productivity in an eco-friendly manner as this approach has the potential to supersede the ecological barriers enforced by native soil microbiota, and also efficiently overcome the adverse impacts of climate change, leading to improved plant health (Del Carmen Orozco-Mosqueda et al., 2018; Rodriguez & Durán, 2020). In recent times, the concept of targeted genetic engineering of phytomicrobiomes is also emerging as a means of long-term agricultural sustenance (Ke et al., 2021).

Microbiome-based approach of rhizospheric engineering for abiotic stress mitigation

Conventionally, microbiome-based approach for rhizospheric engineering involved the implementation of microbial inoculants like plant growth-promoting rhizobacteria, endophytes, AMF as biofertilizers or even recombinant microbial strains for improving crop health and productivity, establishing disease biocontrol (Begum et al., 2019; Chaparro et al., 2012; Ryan et al., 2009). Traditional methods also involved disassembling microbial communities by physical means like tillage, use of antibiotics, etc. to allow propagation of plant beneficial microbial communities (Brussaard et al., 2007).

Recently, the focus on the microbiome-based approach of rhizospheric engineering has undergone a paradigm shift from the application of bioinoculants to modulating of rhizospheric soil microbiome majorly by two approaches, viz. application of synthetic microbial communities/consortia (SMC) or acclimatization of the rhizospheric soil microbiome to any adaptive trait using plant-mediated artificial selection/multi-passaging approach over successive plant growth cycles (Dubey & Sharma, 2021; Liu et al., 2020). Strategic manipulation of the rhizospheric microbiome requires an advanced understanding of the mode of action of beneficial root-associated microbiota and identification of key root exudates, which can play integral roles in mediating plant disease suppression and crop improvement (Pascale et al., 2020).

Comprehensive reviews have pinpointed several factors determining the rhizospheric microbiome assembly, and stressed upon the importance of smart manipulation of plant rhizospheric microbiomes using a systems-based approach (Chaudhary et al., 2021; de Faria et al., 2020; Dubey & Sharma, 2021; Hakim et al., 2021; Kaul et al., 2021; Liu et al., 2020; Mitter et al., 2019; Mohanram & Kumar, 2019; Qu et al., 2020; Rodriguez et al., 2019; Song et al., 2020). Such an approach can integrate the knowledge gained from perspectives of plant immunity, physiology, genetics, and plant-microbe interactions, to derive eco-friendly and efficacious stress management practices for diverse agro-ecosystems.

Synthetic microbial communities/consortia (SMC) for rhizospheric engineering

The plant microbiome is a highly complex association of numerous microbes that help the plants in various beneficial ways. The functions performed by members of the microbiome include improved growth and development of the plant, induction of resistance against phytopathogens, and tolerance towards various stresses (Compant et al., 2019). However, these functions are performed by only a few microbial species and not all the members of the microbiome. The synergistic and additive effects of these few key members are responsible for the traits beneficial to the plant. Thus, these few key members can be used in designing a robust SMC.

The application of SMC can overcome the limitations faced by conventional bioinoculants. Unlike single strain bioinoculants, SMCs can accomplish complex tasks through the division of labour between interacting microbial populations and that too in an expedited manner. Another critical feature of SMC is its resistance to being outcompeted by other species as compared to bioinoculants (Alnahhas et al., 2020; Karkaria et al., 2021). In a SMC, the synergistic interactions between microbial members make it more robust whilst offering multiple beneficial traits to the plants. This increased stability and robustness helps a community perform better even under fluctuating environmental conditions (Karkaria et al., 2021; Orozco-Mosqueda et al., 2021).

Construction of SMCs is popularly done by strategically selecting function-specific microbes in bottom-up combinations. Indigenous strains are selected and assembled to construct a community that closely mimics the microbiome of the host. These strains are chosen based on their interactions and plant beneficial attributes, by employing culture-dependent screenings (Armanhi et al. 2018; Compant et al., 2019; Lemanceau et al., 2017; Vorholt et al., 2017). The microbial members in the designed microbial community are expected to act in a synergistic manner to perform various functions, favouring the plants. The SMC may include strains having a similar mode of action but can exhibit tolerance towards different environmental stresses (Compant et al., 2019). Additionally, microbial community profiling is performed to select key members for traits including robust colonization and prevalence across developmental stages (de Souza et al., 2020). However, the constructed community is always less complex than the natural microbiome (Vorholt et al., 2017).

The steps in designing a SMC include extensive studies on the microbiome of the host plant, isolation and identification of the core microbes of the host, screening of microbial strains on the basis of their functions promoting plant attributes, checking the compatibility among the selected microbial strains, and finally assessing the efficacy of the developed community. Detailed investigations on microbe-microbe and plant-microbe interactions are important for the characterization of core microbes. The relationship among selected microbial members should be synergistic and not antagonistic, whilst their combined effect should always favour the host plant (Arif et al., 2020).

Several methodologies have been devised for screening a large number of SMCs, as well as members for constituting SMCs, including microdroplet screening, artificial intelligence and machine learning, deconvolution technique and neural networks for predicting plant phenotypes in the presence of a specific SMC. The droplet-based analysis of microbial communities has gained popularity since it can analyse the SMC based on mutualistic interactions between member strains, wherein microdroplets can be used to co-cultivate microbial strains to detect interactions via fluorescence-based technology (Park et al., 2011). Alternatively, by integrating omics and phenotypic data with the suitable platform, efforts are being made to predict the resilience and functionality of an SMC by machine learning (ML) algorithms and artificial intelligence (AI) (de Souza et al., 2020). In recent times, the iterative deconvolution technique used in combinatorial biochemistry appears to be a suitable method for the constitution of SMCs. Neural networks have also been implemented for the prediction of plant phenotypes in the presence of SMCs, based on the data of plant-bacterium binary interactions (Herrera Paredes et al., 2018).

Efforts have been made towards the development and testing of SMCs for various hosts for enhancement of plant growth and mitigation of abiotic stresses. Rolli et al. (2015) constructed a SMC including strains of *Acinetobacter*, *Bacillus*, *Sphingobacterium*, *Enterobacter*, and *Delftia*. The community was reported to confer drought tolerance traits in grapevine cultivar *Barbera*. They also reported plant growth promotion activities in capsicum, under water stress. Molina-Romero et al. (2017) designed a SMC including strains of *Pseudomonas putida*, *Sphingomonas*, *Azospirillum brasilense*, and *Acinetobacter* for blue maize. In normally hydrated conditions, seeds inoculated with designed SMC enhanced the dry weight of root and shoot, and plant height compared to the mono-inoculation treatments or uninoculated controls, whereas, under drought conditions, improved plant stress tolerance was reported. Zhuang et al. (2020) constructed a SMC consisting of six *Pseudomonas* strains isolated from the rhizosphere of Jinxiang garlic, which showed plant growth-promoting activity in radish seedlings. Interestingly, they also emphasized the fact that the rhizosphere of most plants has *Pseudomonas* as a native member, so the designed SMC can survive in the rhizosphere of multiple host plants and exhibit plant growth-promoting ability (Zhuang et al., 2020). Armanhi et al. (2018) created a community-based culture collection from sugarcane rhizospheric microbiome and used naturally occurring and highly abundant bacterial genera from roots and stalks of sugarcane to construct a SMC. The application of this abundance-based SMC in maize resulted in enhanced plant biomass, indicating the successful replacement of maize rhizospheric microbiome. This suggested that abundance-based SMC can be suitably applied to diverse plant systems for agronomic improvements.

In another report, different combinations of bacterial strains as potent SMCs were able to modify phosphate accumulation in the *Arabidopsis thaliana* shoot tissues, thereby leading to alterations in plant phenotype under phosphate starvation conditions (Herrera Paredes et al., 2018). This implied that plants modulate their rhizospheric microbiome to recruit/assemble specific stress-resistant microbes which can induce plant defence and increase the chances of their survivability. Evidence from the studies indicates that deciphering the interactions between rhizospheric microbiomes and respective host phenotypes is crucial for customizing simplistic SMCs, which can be realistically used for achieving any desired plant phenotype, e.g., stress tolerance and/or enhanced crop yield. Table 1 is a compilation of studies on the generation of SMC for abiotic stress management, with their respective plant system.

Host-mediated artificial selection: Top-down approach of rhizospheric engineering

It has been established that the plant genotype affects the microbial composition in the rhizosphere, with root exudates being a strong determinant of the same (Mitter et al., 2017). In the top-down approach, the natural microbiome associated with the host is tailored in situ, by manipulating one or more factors related to the ecosystem. The modulation of such factors in the ecosystem drives the evolution of the microbiome, leading to attainment of the desired trait. This approach facilitates the study of the dynamics of the microbiome at molecular level, using various omics techniques, under the influence of definite factors (Ke et al., 2021; Lawson et al., 2019). It enables the host plant to screen the microbiome under selection pressure, and select the microbes that confer either stress tolerance, biocontrol attributes, or plant growth-promoting properties to plants (Arif et al., 2020). Host-mediated artificial selection aims at the targeted evolution of the microbiome to enhance the overall performance of the plant, which is the key parameter used to indirectly measure the efficacy of the microbiome (Mueller & Sachs, 2015). This method involves the setting up of a multi-passaging experiment to screen for the microbiome having the desired phenotype. Over repeated plant growth cycles, the most suitable microbiome is chosen from the best-performing plants for application as inoculum for subsequent passages. Thus, this method employs the propagation of the desired phenotype of the host plant. The application of best-performing microbiomes in successive cycles leads to gradual evolution and domestication of the microbiome that can best benefit the selected plant phenotype.

The main advantage of this approach over generation of SMCs is that the microbial candidates are pre-selected by the host and already adapted to the existing stress conditions. In SMCs, the candidate microbes are first assessed on the basis of their host-favouring properties under conditions that mimic the field environment but are less complex, and then the SMCs are constructed (Compant et al., 2019). However, SMCs include only the culturable microbes, whilst the host-mediated approach employs both culturables and as-yet unculturable microbes (Dubey & Sharma, 2019).

An experiment based on multiple plant growth cycles was set-up for the model organism *Arabidopsis thaliana* to demonstrate the success of implementing a host-mediated artificial selection approach (Panke-Buisse et al., 2015, 2017). The experiment was used to screen and select the microbiome influencing early and late flowering trait in *Arabidopsis*. It was carried out till 10 cycles of plant growth and the four best-performing microbiomes were selected on the basis of desirable phenotype. The selected microbiome was inoculated in related crucifers that resulted in altered flowering time. A greater abundance of inflorescence was observed in plants inoculated with a late flowering microbiome. This experiment paves way for future studies that can direct targeted evolution in host plants to enhance crop productivity. An interesting study highlighted that successive passaging of the rhizospheric microbiome of tomatoes in modern and wild cultivars resulted in highly genotype-specific microbiome assembly (Cordovez et al., 2021).

The multi-passaging approach of rhizospheric engineering has been demonstrated to mitigate different abiotic stresses in plants. Successive passaging of rhizospheric soil microbiome for three plant growth cycles led to the co-evolution of plant and rhizospheric microbial communities (Lau & Lennon, 2012). It eventually resulted in enhanced plant fitness under drought stress in field mustard, by directly inducing dynamic changes in bacterial and fungal communities. Employing an improvised method, terHorst et al. (2014) used an equal proportion of rhizospheric microbiome/mesocosms with sterile soil for application in three plant growth cycles under selection pressure (drought stress) to achieve stress tolerance in field mustard. This study suggested that both ecological and evolutionary responses contribute equally to modulating plant's stress adaptation (terHorst et al., 2014). More recently, the multi-passaging approach that extended to six plant growth cycles, were observed to be potent enough to confer drought resistance in the host plant *Triticum aestivum* (Jochum et al., 2019). The 16S rRNA amplicon sequencing of the artificially selected microbiome revealed the abundance of *Proteobacteria* at the phylum level, specifically β-*Proteobacteria* (Jochum et al., 2019).

Mueller et al. (2021) coined the term “differential microbiome-propagation” method for artificial indirect selection of rhizospheric microbiomes and demonstrated improved salt stress tolerance in host plant *Brachypodium distachyon* using this method. Mitigation of salinity stress in *Vigna radiata* was witnessed when Anand et al. (2021) attempted to adapt the rhizospheric microbiome of the host

TABLE 1 Management of abiotic stresses by synthetic microbial communities/consortia (SMC) for agricultural sustainability

Plant system	Members of SMC	Stress	References
Lactuca sativa var. *longifolia* cv. White Paris	Native consortium of AMF	Salinity stress tolerance by ionic homeostasis	Santander et al. (2019)
Phoenix dactylifera cv. Boufeggous	Indigenous species *Glomus* sp., *Sclerocystis* sp., and *Acaulospora* sp.	Management of salinity stress with enhanced plant physiology	Ait-El-Mokhtar et al. (2019)
Populus deltoides X *P. nigra* clone	Strains of *Acinetobacter calcoaceticus*, *Burkholderia* sp., *Burkholderia vietnamiensis*, *Curtobacterium* sp., *Enterobacter asburiae*, *Pseudomonas* sp., *Rahnella* sp., *Rhizobium tropici*, *Rhodotorula graminis*, *Sphingomonas yanoikuyae*	Drought stress tolerance and plant growth-promoting activity enhanced root and shoot biomass, and total plant nitrogen compared to control plants	Khan et al. (2016)
Trigonella foenum-graecum var. Giza 30	*Glomus monosporum*, *G. clarum*, *Gigaspora nigra*, and *Acaulospora laevis*	Tolerance against cadmium stress	Abdelhameed and Rabab (2019)
Vitis vinifera cv. Barbera	Strains of *Acinetobacter*, *Bacillus*, *Sphingobacterium*, *Enterobacter* and *Delftia*	Tolerance to drought stress by improved water holding capacity and reduction in water loss during desiccation. Root biomass increased two-fold compared to untreated plants	Rolli et al. (2015)
Zea mays	Strains of *Pseudomonas putida*, *Sphingomonas*, *Azospirillum brasilense*, and *Acinetobacter*	Drought stress tolerance with enhanced plant height compared to mono-inoculated and uninoculated plants	Molina-Romero et al. (2017)
Zea mays	Strains of *Asticcacaulis*, *Bosea*, *Burkholderia*, *Dyella*, *Chitinophaga*, *Ensifer*, *Enterobacter*, *Lysobacter*, *Microbacterium*, *Pantoea*, *Pedobacter*, *Pseudoxanthomonas*, *Rhizobium*, *Sphingomonas*, *Stenotrophomonas*, and 2 unidentified genera of *Comamonadaceae* and *Streptomycetaceae*	Plant growth promoting activity with an increase in biomass by 3.4 fold, dark green leaves and increased branched roots in inoculated plants as compared to uninoculated plants	Armanhi et al. (2018)

plant, to salt stress via host-mediated artificial selection by multiple rounds of plant growth under selection pressure (salinity). The analysis of salt stress tolerance, conferred by the adapted microbial community, was performed by assessing parameters including plant biometrics, stress markers, and bacterial diversity (Anand et al., 2021, Dubey et al., 2022). Similarly, the multi-passaging approach of rhizospheric engineering was successfully coupled with the ramping-up of salinity stress, and implemented for nine plant growth cycles, in *Brachypodium distachyon*, which resulted in salinity stress tolerance in plants after as early as 1–3 passaging cycles (Mueller et al., 2021). The promising results of the above studies emphasize the potential of microbiome-based approaches to mitigate stress and promote plant growth. Reports on host-mediated artificial selection, with their respective plant system and implications, have been compiled in Table 2.

Stress-mediated alterations in rhizospheric microbiome community

There are several abiotic and biotic factors that govern the dynamic interrelations between plant and associated microbiota, and also determine the organization of plant-associated microbial communities (Jones et al., 2019). In recent times, advanced molecular tools like next-generation sequencing technologies have helped in deciphering the intricacies of diverse plant-microbe interactions across different plant systems under various abiotic stresses (Barea, 2015; Xu, Pierroz, et al., 2021). Some interesting case studies have been discussed below in this context.

Several abiotic stress factors have been reported to alter the root microbiome structure in different plants (Hartman & Tringe, 2019). Specifically, the role of drought has been found to induce changes in the composition of rhizospheric microbiomes and also affect their functionality (Babalola et al., 2021; Song & Haney, 2021; Xie et al., 2021). Similarly, salinity stress also programmes the functionality of rhizospheric microbiomes in different plants (Egamberdieva et al., 2017; Yukun et al., 2021).

The composition of rhizospheric microbiomes associated with rice roots subjected to drought stress was found to be significantly different when compared to rice plants under the recovery phase (Santos-Medellín et al., 2021). Metagenomic analysis indicated that drought-affected rice roots harboured species of *Actinobacteria* in greater abundance, orchestrating the drought stress recovery process in rice (Santos-Medellín et al., 2021). The possible reasons for such alterations under drought stress have been reviewed recently (Naylor & Coleman-Derr, 2018). A meta-analysis of plant-endophyte association under stress conditions

TABLE 2 Acclimatization of microbial communities for stress mitigation by multiple passaging

Plant system	Stress	Response to acclimatization	References
Brassica rapa	Drought stress tolerance	Plant growth parameters like fruit number, flower number, and days to flowering were monitored. Fruit and flower production increased when plants were raised with an adapted microbiome	Lau and Lennon (2012)
Brassica rapa	Drought stress tolerance	The bacterial abundance and richness increased during adaptation. In the case of the fungal community, the richness increased but abundance decreased. There was an increase in soil nitrogen concentration and a reduction in carbon to nitrogen ratio during adaptation	terHorst et al. (2014)
Brachypodium distachyon	Salt stress tolerance	The ramping-up of salinity stress was performed and plant biomass, seed set, stress tolerance phenotypes were recorded. Enhancement in plant biomass and total seed weight was observed upon acclimatization	Mueller et al. (2021)
Triticum aestivum	Drought stress tolerance	Symptom of delayed onset of water-deficit stress was recorded. Shifts in bacterial phyla were observed such as an increase in *Proteobacteria* phylum by 1.2-fold, whereas the relative abundance of *Actinobacteria* and *Acidobacteria* decreased	Jochum et al. (2019)
Vigna radiata	Salt stress tolerance	For first cycle, the microbiome from the plant with the earliest pod development was selected. For subsequent cycles, the microbiome from the inoculum+salt treated plant was used as inoculum. Plant growth parameters and stress marker levels such as proline content, malondialdehyde, total soluble sugar, hydrogen peroxide and antioxidant enzymes were estimated. The reduction in stress markers was observed in microbiome inoculated plants	Anand et al. (2021), Dubey et al. (2022)

revealed the role of endophytes in stress mitigation in different plant systems (Rho et al., 2018).

Meta-omics-based investigations of the rhizospheric microbiome of lettuce and tomato irrigated with wastewater and freshwater revealed enrichment of stress-associated genes in the rhizospheric microbiome of wastewater supplemented plants as compared to freshwater treatment (Zolti et al., 2020). This study highlighted that microbial communities act as microsensors to tap the finer alterations occurring due to varying stresses in host plants. Interestingly, metagenomic analysis of rhizospheric microbiomes from different potato genotypes under stressed and non-stressed conditions revealed that microbes possessing distinct functional genes responsible for formation of biofilm, detoxification of reactive-oxygen species etc. were more prevalent in the rhizospheres of stressed potato plants, signifying the presence of an actively stress-sensing and adapting microbiome in its rhizosphere (Faist et al., 2021). Rhizospheric microbiomes of two lentil cultivars showing differential growth patterns in the rice fallow ecosystem, revealed a highly diverse composition of the microbiomes, which could be correlated with the differential microbial nitrogen and phosphorus metabolism existing in the cultivars (Pramanik et al., 2020). Another comprehensive study revealed that phosphate stress in *Arabidopsis* triggered plant immune response and mediated root microbiome restructuring in the presence of a SMC (Castrillo et al., 2017). A comparative analysis of rhizospheric microbiomes of different peanut cultivars under salt-stressed and non-stressed conditions revealed distinct shifts in the bacterial community diversity (Xu, Ding, et al., 2021). Based on the taxonomical analysis, increased prevalence of bacterial phyla namely *Actinobacteria*, *Proteobacteria*, *Chloroflexi*, *Acidobacteria*, and *Cyanobacteria* was found in rhizospheric soils of peanut. Salt stress induced greater abundance of *Cyanobacteria* and *Proteobacteria*, and lower prevalence of *Acidobacteria*, particularly in salt-tolerant cultivars.

These reports highlight the role of stress factors in triggering changes in the rhizospheric microbiomes of plants. Insights from these studies indicate that strategic manipulation of rhizospheric microbiomes of different crops can result in efficient stress management programmes.

CHALLENGES WITH ENGINEERING OF RHIZOSPHERIC MICROBIOME

Our existing ability to harness and manipulate the rhizospheric microbiome is limited because of several factors. Some of the major challenges impeding the application of rhizospheric microbiome engineering have been described below.

Identification of core microbiome

For the engineering of rhizospheric microbiome, extensive studies on the microbiome of the plant and the interwoven association between microbe-microbe and plant-microbiome are a pre-requisite. The understanding of the core microbiome is restricted to a few host plants (Castellano-Hinojosa & Strauss, 2021), which limits the application of microbiome-based strategies to only selected plants. For a wider outreach, it is important to characterize the core component of the microbiomes of a range of economically important plants from diverse agro-climatic zones (Toju et al., 2018). This will ensure the successful deployment and expansion of rhizospheric engineering for agricultural sustainability.

Development of plant microbiome vaults

There have been initiatives towards generating Microbiome Biobanks, with the Microbiota Vault being one of the first ones to be established for the human microbiome; however, there are several challenges including logistic issues related to storage of microbiomes, which need to be addressed for its success (Ryan et al., 2021). Moreover, plant-microbiome specific databases and biobanks are yet to be developed (Lucaciu et al., 2019). Such a collection will go a long way in bringing rhizospheric microbiome engineering to see the light of the day.

Discrepancy between the outcomes of laboratory and field experiments

The experiments conducted in laboratories are under controlled conditions with optimum concentration of nutrients and defined growth conditions for model organisms. However, the conditions in fields are variable and highly complex. Primarily, the structured community has to endure high microbial diversity, different climatic factors, varied stress conditions and agri-management practices in fields (Sessitsch et al., 2019). Due to these factors, the fate of SMC and artificially selected microbiome by the plants cannot be accurately predicted, and are likely to exhibit positive, neutral or even negative effects.

Attempts to culture the "as yet" unculturables

A common limitation faced by different strategies for rhizospheric engineering is the large, and pertinent fraction of "as-yet" unculturables in the rhizospheric microbiome. Hence, the construction of SMCs is restricted to the strains that can be cultured. Novel methods to enhance the culturability of strains from stress-acclimatized microbiomes will ensure the development of more efficient and sturdy SMCs for stress management (Sarhan et al., 2019; Sergaki et al., 2018).

Logistic issues related to the application of microbiomes

In host-mediated artificial selection, multiple cycles of plant growth are required for the targeted evolution of the microbiome to enhance the performance of the plant. Continuous rounds of plant growth are practically tedious and time-consuming. Moreover, once the microbiome is acclimatized under selection pressure, its further propagation might negatively impact its functionality. However, a major limitation in rhizosphere engineering is the scarcity of preservation methods to

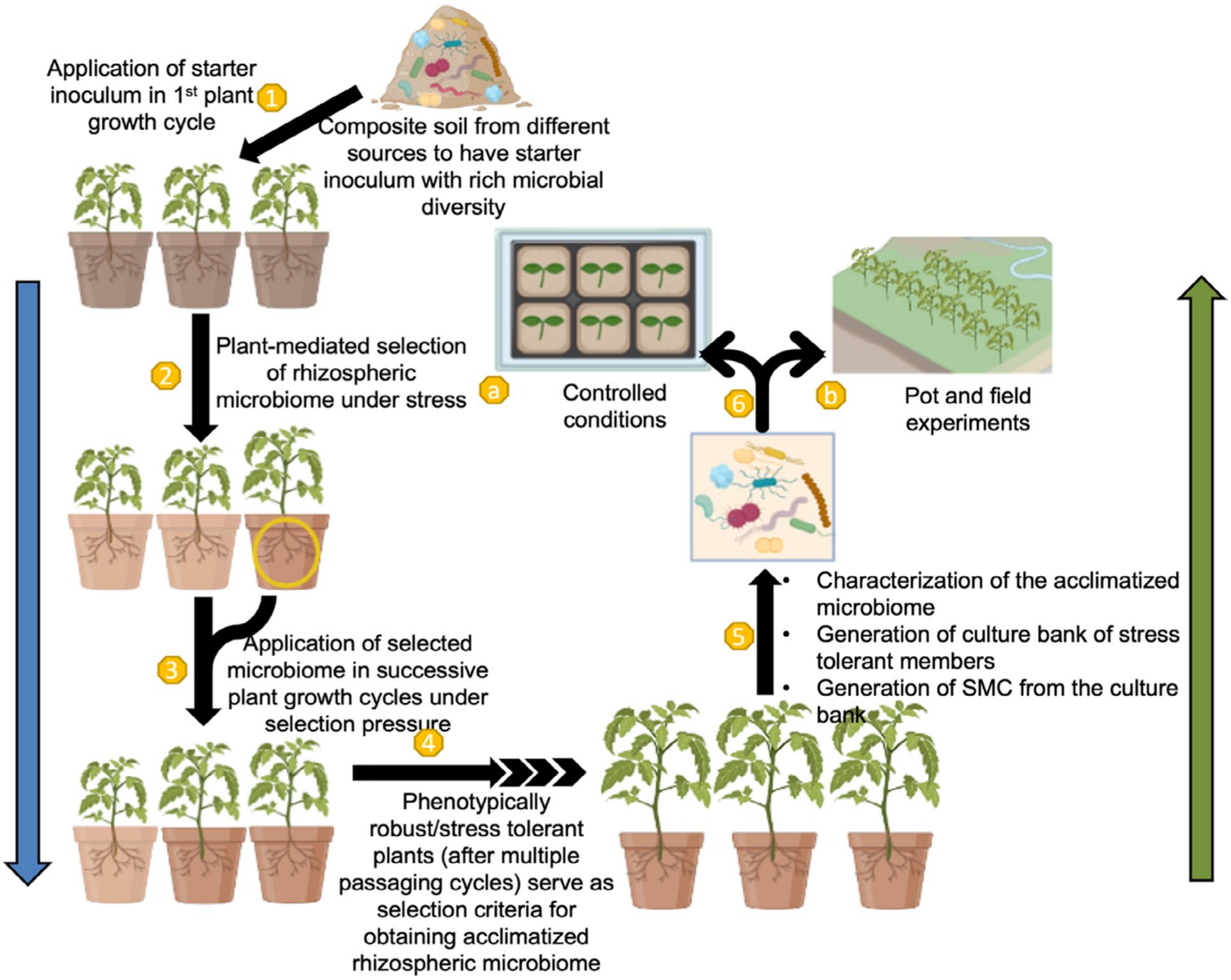

FIGURE 2 Combinational approach for rhizospheric engineering of plants for mitigation of stresses. (1) application of composite soil as starter inoculum having diverse microbes for the first round of plant growth cycle. (2) plants recruit beneficial microbes in the rhizospheric region to enhance their growth and development under stress conditions. (3) the selected microbiome from best-performing plants is applied in successive plant growth cycles exposed to stress. The procedure of multiple passaging continues till an acclimatized microbiome is obtained. (4) phenotypically robust plants from multiple passaging cycles serve as the source for the acclimatized microbiome. (5) the acclimatized microbiome is characterized, and a culture bank of stress-tolerant microorganisms is generated. Generation of synthetic microbial community/consortium (SMC) from the acclimatized microbiome can be done on the basis of functional characterization of selected members of the acclimatized microbiome. (6) application of SMC for agriculture sustenance under stressed conditions is assessed in plant growth experiments under controlled conditions like plant growth chamber (a), and by application of acclimatized microbiome in pots and subsequently in fields (b) (created using BioRender). 🟦Top-down strategy 🟩bottom-up strategy

store the engineered microbiome without disrupting its microbial interactions. The engineered microbiome is less complex than the natural one, nonetheless, it contains diverse microbial genera. Whilst preservation methods for culturable microbes are established, strategies for preserving functional soil microbiomes (including the as-yet unculturables) need to be developed (Bhattacharjee et al., 2022; Prakash et al., 2020). The successful establishment of an engineered microbiome under field conditions requires optimization of various factors including the number of active cells to be applied, growth media for strains, suitable formulations, mode of application etc. All these factors are pertinent for the microbiome to be able to endure the conditions prevalent in the natural environment. Then, tracking of applied engineered microbiome for checking its establishment and efficiency under in vivo conditions is cumbersome (Sessitsch et al., 2019).

BOX 1 Recommendations for future course of action

- Abiotic stress management using bottom-up or top-down approaches of rhizospheric engineering can be endeavoured for a wider range of crops, growing in diverse ecosystems.
- Impact of ramping-up of stress conditions can be assessed to facilitate plant-mediated selection of acclimatized microbiome for alleviation of stresses in economically important cereals and legumes.
- The efficacy of a novel synthetic microbial community/consortium, developed using bottom-up and top-down approaches of rhizospheric engineering, needs to be assessed in natural conditions as a universal stress mitigator.

CONCLUSIONS AND FUTURE PERSPECTIVES

Microbiome-based approaches for engineering the rhizosphere show immense potential in offering services toward sustainable agriculture, with less competition encountered from indigenous microbes, and more adaptability to the plants' environment. However, the area is still in its infancy because of several challenges including limited availability of data about the microbiome of plants, variable results of engineered microbiomes in laboratories and fields, non-availability of preservation methods for whole microbiota, issues related to tracking of microbiome post-application in vivo etc. Complex feedback regulation occurs between plants and rhizospheric microbes in response to abiotic stresses. Elucidating the feedbacks that alter the plant-microbe interactions under non-stressed and stressed conditions, will be vital for developing stress-resilient crops, enhancing crop productivity, improving carbon fixation as well as mediating efficient nutrient cycling in soil (de Vries et al., 2020). Besides, research needs to be prioritized towards developing model host-microbiome systems, and fine-tuning optimal methods for assemblage and application of rhizospheric microbiome in diverse agro-ecosystems (Busby et al., 2017). Selection pressures, including stress conditions, play crucial roles in modulating the rhizospheric community structure and controlling microbial functionality, even governing plant immune responses. Reductionist approaches focus on the application of selected potent microbes from the rhizosphere, which can mimic the responses of the rhizospheric microbiome of plants under natural conditions (Fitzpatrick et al., 2020). Combinational application of ecological and reductionist strategies is expected to harness maximum benefits for combating challenges prevailing in diverse agroecosystems (Figure 2). Some recommendations for the future course of action have been enlisted in Box 1. Endeavours should be directed towards adopting a multi-disciplinary approach for understanding the intricacies of plant-microbiome interactions and tapping the potential of rhizospheric engineering for efficacious stress management and agronomic improvements.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable - no new data generated

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