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Plant growth-promoting rhizobacteria for orphan legume production: Focus on yield and disease resistance in Bambara groundnut

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Orphan legumes are now experiencing growing demand due to the constraints on available major food crops. However, due to focus on major food crops, little research has been conducted on orphan legumes compared to major food crops, especially in microbiome application to improve growth and yield. Recent developments have demonstrated the enormous potential of beneficial microbes in growth promotion and resistance to stress and diseases. Hence, the focus of this perspective is to examine the potential of plant growth promoting rhizobacteria (PGPR) to improve Bambara groundnut yield and quality. Further insights into the potential use of PGPR as a biological control agent in the crop are discussed. Finally, three PGPR genera commonly associated with plant growth and disease resistance (*Bacillus*, *Pseudomonas*, and *Streptomyces*) were highlighted as case studies for the growth promotion and disease control in BGN production.

KEYWORDS

***Bacillus*, Bambara groundnut, food security, plant growth promoting bacteria, *Pseudomonas*, *Streptomyces*, sub-Saharan Africa**

Introduction

Food security is the ability of a population to access and afford enough food to live a healthy life (Olanrewaju et al., 2022). Climate change poses a significant threat to achieving food security, especially in developing countries. Rising temperatures and extreme weather events have caused droughts, floods, and increased soil salinity, which have reduced crop yields and caused food prices to spike. The impacts of climate change on our food system are already being felt in communities across developing countries (Lenaerts et al., 2019). Food security in sub-Saharan Africa is already threatened by climate change. As temperatures increase and rainfall patterns change, sub-Saharan Africa is expected to experience droughts and floods that will reduce crop yields, damage infrastructure, and drive-up food prices. These climate-induced shocks will have a devastating impact on people, many of whom live in poverty and cannot afford more food. The impact of climate change on food production in sub-Saharan Africa has led to programs such as the food for progress initiative, purchase for progress initiative, and other programs which are working to help smallholder farmers in sub-Saharan Africa improve their access to markets and invest in climate-resilient technologies, like drip irrigation systems (Crocker, 1986; Devereux, 2016).

Orphan legumes are a group of important but neglected crops that are an important part of a food-secure diet. Orphan legumes are also an important part of sub-Saharan African diets, as they are a nutritious source of protein, calcium, and other essential nutrients (Cullis and Kunert, 2017). In addition to climate change impacts, food security is threatened by a lack of research and investment in orphan legumes. The protein- and nutrient-rich seeds of orphan legume crops can be used to make flour and animal feed (Tadele, 2009; Adebowale et al., 2011; Adebola et al., 2017; Ruckle et al., 2017; Adeleke et al., 2018; Afolabi et al., 2018; Lambein et al., 2019; Oluwole et al., 2021). They include Bambara groundnut, African yam bean, winged bean, marama bean, grass pea, chick pea, and cowpea, among others.

In search of ways to mitigate climate change impact on food crops, use of beneficial microorganisms has become as important as any other form of plant improvement program. Many microorganisms have been used to make products, such as, nodumax and biofix, which have improved plant production (Akley et al., 2022). While there is a healthy debate about which plants are most important in the food system, the fact that plant-microbe interactions play a key role in the food system is undeniable. The variety of plants and microbial species that interact with one another in the food system is enormous. This means that an enormous amount of research is being done to identify the specific microbes that are involved in specific plant processes. The primary food source for these microbes in the rhizosphere is plant biomass. Plant microorganisms are a major component of the ecosystem and the food chain for all organisms on the planet. Incorporating plant-microbe interaction research into orphan legume crop production will be a great advancement in the production of these crops. We will focus on Bambara groundnut in this review as it is fast receiving improved research activities, but only one research on its microbiome has been reported so far (Ajilogba et al., 2022b).

Bambara groundnut (BGN) production is drawing attention, especially in sub-Saharan Africa, because it can be used as food, fiber, and medicine (Jideani and Jideani, 2021; Ajilogba et al., 2022a). The demand for BGN is increasing because of its high nutritional value and increasingly recognized medicinal value, which makes it a preferable alternative to the major crops.

Because of the absence of a well-annotated reference genome, studies have attempted to determine which elements of cultivation and genetics contribute to BGN traits by comparing them with the genomes of closely related crops (Ho et al., 2017). Hence, molecular markers have been developed in various studies (Molosiwa et al., 2015; Fatimah and Ardiarini, 2018). BGN yield is influenced by photoperiodism and plant density (Kendabie et al., 2020). However, little research has been conducted regarding the response of yield and other BGN traits to the application of plant-growth promoting rhizobacteria (PGPR), although studies have extensively demonstrated the importance of PGPR in the production of many crop species (Olanrewaju, 2016; Olanrewaju and Babalola, 2019a; Lee et al., 2020). For example, the priming of plant seeds with PGPR and the application of PGPR to plant roots reportedly stimulate plant growth through the production of nutrients and pathogen controlling metabolites. In addition, PGPR can improve tolerance to abiotic (e.g., drought and salinity) and biotic stresses (e.g., plant pathogens) (Babalola et al., 2019; Ojuederie et al., 2019; Olanrewaju et al., 2021a).

The exploitation of PGPR from orphan legume microbiome will play an important role in BGN production, and there is a clear need to better understand the relationship between the microbiome, BGN yield, and BGN disease resistance. This perspective summarizes the knowledge about the factors that contribute to BGN yield. In addition, we examine the potential role of PGPR, with a focus on *Bacillus*, *Pseudomonas*, and *Streptomyces*; three widely prevalent genera in achieving high yields, improved nutrient profiles, and disease resistance in BGN.

Strategies to increase BGN yield and quality

Production conditions that influence BGN yield and nutrient composition include plant genotype, environmental conditions (such as temperature, water availability, and fertilizer application), photoperiod, and plant development stage (Kendabie et al., 2020; Khan et al., 2020; Obidiebube et al., 2020; Olanrewaju et al., 2021b,c; Ajilogba et al., 2022b). At the physiological level, plant growth regulators can also affect the nutrient composition.

Plant-growth promoting rhizobacteria for BGN production

Plant growth-promoting rhizobacteria are present in plant roots and have been associated with plant growth by providing nutrients for plants, production of growth hormones, induction of the plant immune system, and production of metabolites which support plants against pathogens (Olanrewaju, 2016; Olanrewaju et al., 2017; Backer et al., 2018; Etesami and Maheshwari, 2018; Babalola et al., 2019; Singh et al., 2019; Hakim et al., 2021). PGPR is important for sustainable crop production and achieving food security (Ajilogba et al., 2022a). PGPR for

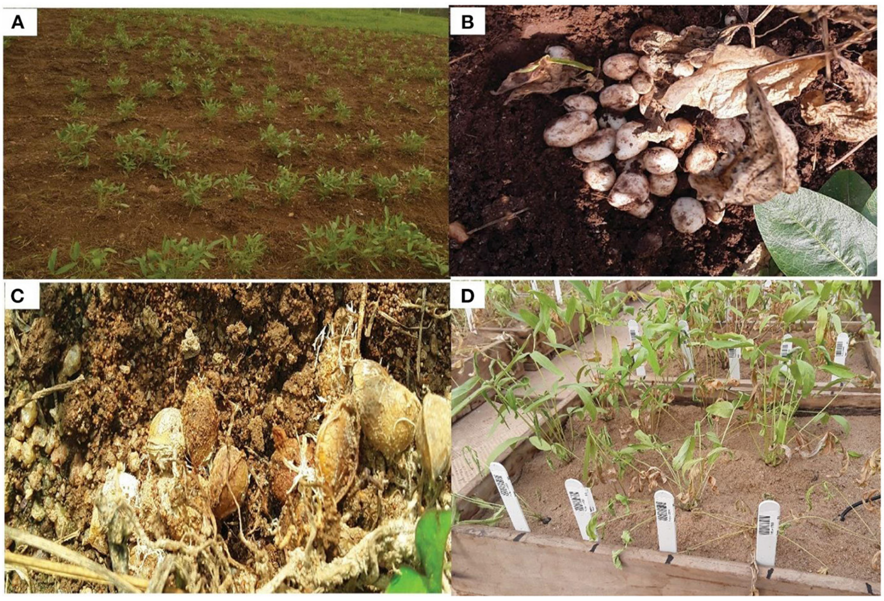

FIGURE 1
(A) Bambara groundnut (BGN) in the field; **(B)** healthy matured BGN pods during harvest; **(C)** infected BGN pods; **(D)** drought stressed BGN plants. [Source: Olanrewaju et al., 2022].

crop yield and quality increase as well as disease/pathogen control has been extensively studied in many crops such as soybean (Silva et al., 2019; Riviezzi et al., 2021), rice (Raja et al., 2017; Xu et al., 2019), maize (Ke et al., 2019; Olanrewaju and Babalola, 2019a; Liu et al., 2020), wheat (Kumar et al., 2018; Ma et al., 2021), chickpea (Laranjeira et al., 2021; Khalifa et al., 2022), and cowpea (Kanthaiah and Velu, 2019; Kumar et al., 2021).

Yield and quality enhancements associated with plant-growth promoting rhizobacteria

Compared to the major food crops, there is relatively little data to support the use of PGPR on BGN production. Most research data on this crop has emerged from evaluation studies for growth traits, nutrient and antinutrient components, antioxidant compositions, and recently, medicinal uses. In the study by Ikenganyia et al. (2017), the effects of bioinoculant methods (soil inoculation and seed inoculation methods) on BGN growth and yield were compared. Both methods increased the yield of BGN, with the soil inoculation method having the highest yield result. Another study by Gomoung et al. (2017) reported the effect of cross inoculation of groundnut and BGN rhizobium on the growth and yield of both crops. Their study further proved that rhizobacteria on a plant species can improve the growth and yield of another plant species. A previous study showed that PGPR improved nutrient acquisition in BGN (Oyewole et al., 2018). Many studies have shown the effect of PGPR on plant growth and nutrient composition (Bakhshandeh et al., 2020; Castaldi et al., 2021; Guo et al., 2021; Kushwaha et al., 2021; Laranjeira et al., 2021); we can therefore postulate that PGPR will improve the nutrient composition and yield of BGN. It is important to determine the impact of PGPR on BGN growth and nutrient composition at various growth stages and different environments.

Our laboratory has already illustrated that bacteria isolated from a plant species or habitat can improve growth promotion and activate stress responses in other plant species (Ndeddy Aka and Babalola, 2016; Olanrewaju and Babalola, 2019a). This means that the tested PGPR can improve BGN growth either in single inoculation or in consortia (Olanrewaju and Babalola, 2019a). As a result, we believe that future research will confirm that PGPR-based inoculants can impact BGN nutrient composition, increase the growth and yield of BGN, promote BGN stress tolerance, and control pathogens.

Biological control and disease resistance associated with plant-growth promoting rhizobacteria

Streptomycetes, *Bacillus*, *Pseudomonas*, *Rhizobium*, and *Azospirillum* are widely used as biocontrol agents (Olanrewaju et al., 2017; Olanrewaju and Babalola, 2019b). Many studies have reported their use in controlling various plant pathogens. For example, by producing the metabolite, wuyiencin, *Streptomyces albulus* CK-15 controls powdery mildew of cucumber (Yang et al., 2021), while *Bacillus* (Cui et al., 2019, 2020; Castaldi et al.,

TABLE 1 Biocontrol activities of *Bacillus* spp., *Pseudomonas* spp., and *Streptomyces* spp. on various plants.

PGPR	Plant	Disease	Pathogen	References
Bacillus subtilis strain Bs-1	Cucumber	Root galls/root knot	*Meloidogyne incognita*	Cao et al., 2019
Bacillus velezensis NKG-2	Tomato	Wilt diseases	*Fusarium oxysporum*	Myo et al., 2019
Bacillus subtilis RH5	Rice	sheath blight	*Rhizoctonia solani*	Jamali et al., 2020
Bacillus amyloquefaciens B9601-Y2	Maize	Leaf blight	*Bipolaris maydis*	Cui et al., 2019
Bacillus amyloquefaciens YN201732	Tobacco	Powdery mildew	*Erysiphe cichoracearum*	Jiao et al., 2021
Pseudomonas stutzeri	Chickpea	Sheath blight	*Fusarium oxysporum* var. ciceri and *Rhizoctonia solani*	Kumar et al., 2022
Pseudomonas aeruginosa CQ-40	Tomato		*Botrytis cinerea*	Wang et al., 2021
Pseudomonas segetis strain P6	Potato and carrot	Soft rot	*Dickeya solani*	Rodríguez et al., 2020
Pseudomonas spp.	Olive	Verticillium wilt	*Verticillium dahlia* kleb	Gómez-Lama Cabanás et al., 2018
Pseudomonas fluorescens ZX	Orange	Blue mold decay	*Penicillium italicum*	Wang et al., 2020
Streptomyces cellulosae isolate Actino 48	Tobacco	Tobacco mosaic virus	*Tobamovirus*	Abo-Zaid et al., 2020
Streptomyces sp. HAAG3-15	Cucumber	Fusarium wilt	*Fusarium oxysporum* f. sp. cucumerinum	Cao et al., 2020
Streptomyces sp. MBFA-172	Straw berry	Anthracnose	*Glomerella cingulata*	Marian et al., 2020
Streptomyces griseocarneus R132	Pepper	Anthracnose	*Colletotrichum gloeosporioides* MPU99, *Colletotrichum guaranicola* INPA2408	Liotti et al., 2019
Streptomyces A1RT	Potato	Potato common scab	*Streptomyces scabies*, *S. turgidiscabies* and *S. stelliscabiei*	Sarwar et al., 2018

2021), *Rhizobium* (Wong et al., 2021; Kawaguchi and Noutoshi, 2022), and *Pseudomonas* (Omoboye et al., 2019; Khalifa et al., 2022) species have been reported in the biocontrol of some plant species.

PGPR acts *via* direct and indirect mechanisms to control plant pathogens. Antibiosis and the production of secondary metabolites that act as toxins to pathogens are examples of direct mechanisms, whereas indirect mechanisms include nutrient competition and the induction of induced systemic resistance (ISR) (Beneduzi et al., 2012; Olanrewaju et al., 2017, 2019; Backer et al., 2018). ISR is strongly connected to the jasmonic acid and ethylene-sensitive pathways (Van Der Ent et al., 2009; Olanrewaju et al., 2019). An effective PGPR must be able to properly colonize its host (Olanrewaju and Babalola, 2019b); hence, PGPR-induced ISR is largely dependent on the rhizobacterium-colonizing ability (Beneduzi et al., 2012). Upon successful activation, ISR can improve the plant's defense capabilities by activating the expression of defense-related genes. Through the production of hormones such as indole acetic acid and gibberellin, PGPR increases the plant's ability to defend against pathogens. ACC-producing PGPR reportedly improves the plant's capacity to produce ethylene and increases its immunity by the induction of ISR (Glick, 2005). However, triggering ethylene and jasmonic acid-dependent plant responses to pathogens does not always correlate with an increase in the phytohormones, as reported in the study by Beneduzi et al. (2012). Hence, PGPR research on BGN should focus on the ability of PGPR to control pathogen infection in BGN through the activation of ISR.

Pathogen control in BGN cultivation: insight into the potential of PGPR applications

The ability of BGN to produce its seeds embedded in the soil has improved its resistance to pest attack but not pathogens. It hosts pathogens varying from bacteria, fungal, virus, and nematode origins, and they have a significant economic impact through yield loss (Figure 1) (Olanrewaju et al., 2022). Brink et al. (2006) reported fungal diseases such as cercospora leaf spot (*Cercospora* spp.), powdery mildew (*Erysiphe polygoni*), and Fusarium wilt (*Fusarium oxysporum*). Fourie et al. (2017) also reported the activities of a root-knot nematode (*Meloidogyne javanica*) on the plant. Pengnoo et al. (2006) also reported the occurrence of leaf blight disease in BGN. In their study, they isolated *Bacillus sp*. strains that were used to control the disease.

It is important to effectively address these threats, to prevent yield losses in BGN production. Biocontrol of pathogens has more advantages for plants, humans, animals, and the environment compared to chemical controls. *Bacillus subtilis* effectively controls leaf blight disease in BGN (Pengnoo et al., 2006), *Meloidogyne incognita* on *Capsicum annuum* cv. Qiemen (Cao et al., 2019) (Table 1).

These results in Table 1 suggest that inoculating BGN with PGPR may assist in controlling disease infestations, representing a substantial advantage over currently available chemical control methods. In addition, consumption of chemical residues through the seeds because of being washed into the soil to the seeds can be eliminated with the application of an effective biocontrol agent. This can be applied as a root trench in place of spraying to minimize damage caused by sprays on young leaves.

Examples of widely prevalent phytomicrobiome members: *Pseudomonas*, *Bacillus*, and *Streptomyces* for growth promotion and disease control in BGN

Pseudomonas spp., *Bacillus* spp., and *Streptomyces* spp. promote plant growth by synthesizing phytohormones, fixing nitrogen, and solubilizing phosphate for plant use (Santoyo et al., 2012; Olanrewaju and Babalola, 2019b). *Pseudomonas* and *Streptomyces* are good plant colonizers and inhibitors of plant pathogens (Olanrewaju et al., 2017). They help the hosts to control pathogens by producing antipathogenic compounds such as siderophores, cyanides, DAPG, antibiotics, lipopeptides, and polysaccharides (Beneduzi et al., 2012; Santoyo et al., 2012). In addition, *Bacillus* make use of their spores as biocontrol agents (Ji et al., 2013).

Studies on various plant species have shown that *Bacillus* spp., *Pseudomonas* spp., and *Streptomyces* spp. can promote plant growth and suppress/control plant diseases (Cui et al., 2019, 2020; Olanrewaju and Babalola, 2019a; Xu et al., 2019; Liu et al., 2020; Yang et al., 2021). The success of plant growth promotion and disease control by PGPR is host-dependent. Studies on *Bacillus* spp. as biocontrol agents have mainly focused on activation of ISR to improve plant resilience, direct plant growth promotion, and aspects of microbial ecology, while studies on *Streptomyces* spp. have mainly focused on its biocontrol ability through the production of secondary metabolites and antibiotics (Olanrewaju and Babalola, 2019b). Inhibition of Fusarium and Armillaria pine rot diseases was inhibited by *Streptomyces kasugaensis* in the study reported by De Vasconcellos and Cardoso (2009). Another study by Wonglom et al. (2019) reported the biological control of leaf spot diseases of *Brassica rapa* subsp. pekinensis by *Streptomyces angustmyceticus* NR8-2.

Overall, previous studies have shown that these three PGPR genera have great promise in promoting plant growth and biocontrol of plant pathogens (Raja et al., 2017; Babalola et al., 2019; Ke et al., 2019; Olanrewaju and Babalola, 2019a,b; Omoboye et al., 2019; Xu et al., 2019; Cui et al., 2020; Guo et al., 2021; Kushwaha et al., 2021; Olanrewaju et al., 2021a; Yang et al., 2021; Khalifa et al., 2022). However, their applications on BGN have not been exploited. Based on a recent study on the microbiome of BGN at various growth stages, these genera are well represented in the rhizosphere of BGN (Ajilogba et al., 2022b). It would be interesting to determine if any strains of these genera can be formulated and tailored specifically for the improvement of BGN yield and disease control.

Conclusions and prospects

BGN is a critical crop for achieving food and nutrition security, particularly in Sub-Saharan Africa and other developing world regions where it is cultivated. Hence, BGN is fast becoming an important crop. Hence, BGN is fast becoming an important crop. PGPR has been associated with benefits such as nutrient mobilization, phytohormone production, stress mitigation, and biocontrol abilities. As a result, studying PGPR inoculants on BGN can increase yield in an environmentally sustainable manner. The microbiome has enormous potential for improving BGN production by increasing yield, mitigating drought stress, and controlling disease.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

OSO researched the data, wrote, and edited the manuscript. OOB supervised the writing of the manuscript. Both authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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