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SPECIALTY SECTION

This article was submitted to
Plant-Soil Interactions,
a section of the journal
Frontiers in Agronomy

RECEIVED 27 July 2022

ACCEPTED 12 September 2022

PUBLISHED 29 September 2022

CITATION

Fwanyanga FM, Horn LN, Sibanda T
and Reinhold-Hurek B (2022)
Prospects of rhizobial inoculant
technology on Bambara groundnut
crop production and growth.
Front. Agron. 4:1004771.
doi: 10.3389/fagro.2022.1004771

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Prospects of rhizobial inoculant technology on Bambara groundnut crop production and growth

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After peanuts and cowpeas (*Vigna unguiculata*), the Bambara groundnut (*Vigna subterranea* (L.) Verdc) is the third most significant food legume in Africa. It is characteristically grown in marginal soils, is drought tolerant, and also has the potential for nitrogen fixation. Despite that, year-on-year Bambara groundnut yields are on a gradual decline due to a combination of abiotic and biotic stresses such as uneven annual rainfall and climate-induced changes in soil microbial community compositions, negatively impacting food security. Thus, the application of rhizobial inoculants at planting significantly improves yields in many leguminous crops. Moreover, symbiotic inoculants are well established in developed countries for improving nitrogen fixation and productivity in grain legumes. Sub-Saharan African countries, however, still under-utilise the above practice. In crop production, nitrogen (N) is the most frequently deficient nutrient since it stimulates root and shoots growth. Whereas nitrogen fertilisers can be used to supplement soil N levels, they are, however, also costly, at times inadequate, may not be timely in supply and may have deleterious environmental consequences. Hence, rhizobial inoculants are seen as a cheaper, easier, and safer method for improving N-fixation and crop productivity in grain legumes, as a result, smallholder farming systems are food secure. Thus, identifying the most efficient rhizobial strains for biofertiliser production for Bambara groundnut is of utmost importance to the farming communities.

KEYWORDS

Bambara groundnuts, food security, legumes (Fabaceae), productivity, biofertiliser, rhizobia

Introduction

Leguminosae, which has more than 770 genera and 19,500 species, is the third-largest land plant family (Liu et al., 2011; Ren, 2018). Additionally, behind cereals, leguminous are the second-most produced crops (Belete et al., 2019). There are many native legume species in Africa where the highest levels of global legume diversity are found (Sprent et al., 2010). According to Mfilinge et al. (2014); Büchi et al. (2015); Phillips and Saunders (2016), and other sources, legumes are grown as fodder, seed crops, as cover crops along cash crops or in conjunction with other crops. The capacity of legumes to fix atmospheric nitrogen has been credited with their ability to dominate many unfavourable and disturbed ecosystems by enabling the plants to flourish in nutrient-poor soils (Andrews and Andrews, 2017; Jaiswal and Dakora, 2019; Van Wyk, 2019).

The Bambara groundnut (*Vigna subterranea* (L.) Verdc) is one of the legumes that were historically grown for food in Africa. Despite being significant in several areas, including nutrition, medicine, and agronomical value, the crop is neglected and underutilised (Musa et al., 2016; Babalola et al., 2017; Gbaguidi et al., 2018; Ikenganyia et al., 2018; Khan et al., 2021). After the well-known groundnut (*Arachis hypogea*) and cowpea (*Vigna unguiculata*), it is the third-grain legume crop grown in the tropical lowlands of Africa (Egbe et al., 2013). The grains show a variety of colours (Figure 1). Bambara groundnuts variety are enjoyed by many people, especially in Africa, and are consumed in various forms, including dried, freshly cooked, and combined with other grains as food (Kanonge-Mafaune et al., 2018). In addition to other nutritional content, the grain of Bambara is made up of a high percentage of protein (20.6%), carbohydrate (56.5%), fat (6.6%), and fibre (6.3%) (Hillocks et al., 2012; Mubaiwa et al., 2017; Ibny et al., 2019). According to Mubaiwa et al. (2017), the Bambara groundnut has a higher protein quality since its protein score recorded was 80% as opposed to 74% for soybean, 65% for groundnut, and 64% for cowpea. The lack of information regarding better seed systems,

breeding, agronomic techniques, processing, and utilisation are amongst the factors restricting the utilisation of Bambara groundnut (Mubaiwa et al., 2018; Tan et al., 2020). It is well known that Bambara groundnut cultivation contributes to the preservation of soil fertility through the symbiotic fixation of nitrogen by root nodule-associated bacterial symbionts called rhizobia (Karunaratne et al., 2015). Despite its contribution to soil wellbeing, symbiotic nitrogen fixation is affected by some climatic conditions such as poor rainfall, prolonged drought, as well as high temperatures that affect rhizobium populations in the soil, and consequently reduce nodulation and yields of locally cultivated Bambara groundnuts (Grönemeyer et al., 2014). As a countermeasure strategy, studies have indicated that coating Bambara groundnut seeds with rhizobial inoculants before planting tends to increase yields (Hillocks et al., 2012; Ibny et al., 2019). Motivated by the need for adaptation to climate change and to sustainably stabilise and improve yield of nutritious food in smallholder agriculture facing challenges to apply N fertiliser (Pulido-Suárez et al., 2021), this review discusses benefits of Bambara groundnut and potential of rhizobial inoculation in Bambara groundnut crop production, and urges on developing adapted inoculants. As a search strategy, we used the terms 'Bambara groundnut', 'rhizobia', 'biofertiliser/inoculants' or 'Biological Nitrogen Fixation', to screen the relevant journals for recent articles from 2010 to 2022, with the exception of one article from 1997. The quality areas of selection bias, suitable data collection and analysis, and generalizability were used to evaluate each study's quality.

Origin and distribution of Bambara groundnut

Bambara groundnut, which is a native African legume, has been grown for generations in sub-Saharan Africa, primarily in semi-arid areas (Ikenganyia et al., 2017; Temegne et al., 2018).



FIGURE 1

Examples of Bambara groundnuts. (A) Dehulled grains in various colours, here from cream to dark brown. (B) Freshly harvested Bambara groundnuts. (C) Symbiotic root nodules of field-grown Bambara groundnut.

According to Nassé et al. (2019); Mayes et al. (2019) and Khan et al. (2021), Bambara groundnut was initially discovered in West Africa and appears to have moved southwards throughout sub-Saharan Africa. Literature has suggested that the Bambara groundnut originated in an area named “BAM-BARA”, which is home to an agriculturist tribe that resided largely in the state of Bambara near Timbukutu in the west African region of central Mali (Tan et al., 2020), hence the name Bambara groundnut. Currently, the Bambara groundnut is grown extensively in most of West to southern Africa, Central Africa, Indonesia, Malaysia, India, Sri Lanka, Philippines, South Pacific, sections of northern Australia, Papua New Guinea, Central and South America (Aviara et al., 2013; Karunaratne et al., 2015).

Several semi-arid and sub-Sahara African countries, including Nigeria, Ghana, Cameroon, Togo, and Mali are now well-known for cultivating the crop. The primary growing regions for Bambara nuts in Southern Africa, are South Africa and Zimbabwe, while Southeast Asia, especially Thailand, Indonesia, and Malaysia, make up the secondary growing region (Khan et al., 2021). The world’s annual production is estimated to be around 330 thousand tons, with the west African countries - Burkina Faso, Cameroon, Mali, Niger, Togo, and the Democratic Republic of the Congo being the major growing regions, with annual production at about 0.3 million tons and with Burkina Faso providing the most extensive yield at around 0.1 million tons per year (Khan et al., 2021). The lower yields in Sub-Saharan Africa emphasise the need for Bambara groundnut breeding to enrich varieties, as well as inoculant use to improve agronomic practices and enhance yields.

Biological nitrogen fixation

The primary nutrient that promotes plant root and shoots development is Nitrogen (N) (Yakubu et al., 2010). Despite its importance, N remains the most often inadequate nutrient for crop production in many parts of the world, especially in Africa and amongst resource-poor farmers. The ongoing use of N fertilisers to supplement N for plants demonstrates the necessity of this nutrient. Pulido-Suárez et al. (2021) and Wekesa et al. (2021) claim that the use of N fertilisers by resource-poor farmers is challenged by several factors such as cost, the possibility they may not be timely available in smallholder farming systems and may leach into surface and groundwater systems, especially when applied in sandy soils. To protect the environment from such unintended consequences, the greening revolution demands that economic, environmental, and renewable energy concerns employ biological alternatives (Gopalakrishnan et al., 2015). Hence, various research initiatives are being directed to the importance of biological nitrogen fixation (BNF), particularly by leguminous crops (Rao, 2014).

BNF is a fascinating biological phenomenon that involves the interaction between soil microorganisms, in particular

bacteria, and higher plants (Santos et al., 2019). When the bacteria are in a symbiotic relationship, the BNF process is mediated by bacteria and the product is readily available to plants (Santi et al., 2013). During this process atmospheric N₂ is reduced to ammonia by the action of the enzyme nitrogenase (Liu et al., 2016). BNF occurs in the rhizosphere of non-leguminous plants and, in the root nodules of leguminous plants in the soil (Ahemad and Kibret, 2014). Rhizobia in the root nodule obtain carbon sources and thus energy from the higher plant and use them to reduce usable N (ammonium) which is then directly supplied to the plant to produce biomass and food (Puozaa et al., 2017; Mahmud et al., 2020). According to Jaiswal et al. (2021), legume-rhizobia symbiosis is responsible for between one-third and one-half of the total N added to agricultural land. Similar to this, Kanonge-Mafaune et al. (2018) claimed that under ideal conditions, grain legumes may fix up to 200 kg of N ha⁻¹, considerably lowering the need for inorganic N fertilisers. Ibny et al. (2019) and Pulido-Suárez et al. (2021) also argue that the nitrogen fixed by legumes can be as high as the amounts of nitrogen fertilisers used in conventional farming practices. This is congruent with Egbe et al. (2013) arguing that nearly half of the amount of nitrogen (N) used in inorganic N fertilisers is through symbiotic nitrogen fixation, according to estimates. According to some estimations, Bambara groundnuts may fix up to 28.42 kg N/ha in the Sudano-Sahelian zone of Nigeria (Yakubu et al., 2010). According to Yusif et al. (2016), fixation by rhizobia recruited from the soil alone provided additional nitrogen of 61.1 mg plant⁻¹, but soil and inoculated rhizobia (HISTICK) together gave an additional nitrogen input of 124.7 mg plant⁻¹ in groundnut in Nigeria. While the above estimates differ in magnitude, the overall observation is that BNF significantly contributes to soil N build-up, making it a reliable substitute for inorganic fertiliser application.

Table S1 presents some of the benefit increases of legume yields or nitrogen inputs with different inoculants. The highest N increases have been recorded by Denton et al. (2017) in Faba bean and Lupin. Furthermore, several reports have as well indicated increased grain yield with increased N content in the soil. The highest grain yield improvements have been recorded in cowpea which was inoculated with *Bradyrhizobium* strains BR 3267 and BR 3262 (EMBRAPA BRAZIL). From the review, it is evident that Bambara groundnut has been ignored by research given that there are few reports on inoculant use on Bambara groundnut. However, the information emanating from research findings on other legume crops is giving support to inoculant technology and its benefit to the plants.

The rhizobial symbionts

According to Tsukanova et al. (2017), rhizobia are soil-borne bacteria that are part of the *Proteobacteria* families α , β , and δ

with the ability to develop nodules on the roots, and occasionally the stems of host plants, which are mostly legumes (Ahemad and Kibret, 2014; Raissa et al., 2020). The alpha-proteobacteria harbour most bacterial genera of nodule-forming microsymbionts; for example, the major genera are *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Mesorhizobium*, *Ensifer* (*Sinorhizobium*), *Neorhizobium*, *Pararhizobium*, and *Allorhizobium*, collectively referred to as “rhizobia” (Jaiswal et al., 2021), which can form symbiotic associations with a variety of legumes.

Except for a few studies that have demonstrated that species of the genus *Bradyrhizobium* nodulate Bambara groundnut, there is little information available on the biodiversity of rhizobia nodulating Bambara groundnut in African soils (Ibny et al., 2019). According to Jaiswal and Dakora (2019), *Bradyrhizobium* is regarded as one of the most cosmopolitan and diverse bacterial groups responsible for nodulation in a variety of host legumes including Bambara groundnut in Africa. However, it is important to remember that the distribution patterns of rhizobial species vary depending on the geographic region (Ikenganyia et al., 2017). Hence, they might be other rhizobial symbionts associated with Bambara groundnut which have not been explored. Despite the need for increased food legume production, it has been reported that the diversity and distribution of the African nodulating indigenous legumes that form symbioses with bradyrhizobia and other rhizobia are not well understood. Nonetheless, research has revealed that bradyrhizobia nodulates several African dietary legumes (Ibny et al., 2019; Ajayi et al., 2020; Dlamini et al., 2021). This could be explained by the distinctive edaphoclimatic conditions of the continent’s diverse habitats (Jaiswal and Dakora, 2019). To find rhizobia that can efficiently nodulate and promote the growth of significant yet underutilised crop species like Bambara groundnut, it is crucial to constantly investigate new geographic regions. Further research to facilitate identifying of numerous unique bradyrhizobia residing in African soils are required, to better understand the biogeography of *Bradyrhizobium* strains and their potential for inoculant production. Examples of some of the rhizobia that have been isolated from different legume crops and more specifically on Bambara groundnut are presented in Table S2. Amongst at least 10 species of *Bradyrhizobium* spp. isolated from nodules or nodulating Bambara groundnut in the laboratory, there are several that were Namibian isolates recently described as novel species, such as *B. subterraneum* (Grönemeyer et al., 2015a), *B. kavangense* (Grönemeyer et al., 2015b), *B. namibiense* (Grönemeyer et al., 2017), or *B. vignae* (Grönemeyer et al., 2016). Thus, this host plant appears to be quite promiscuous towards *Bradyrhizobium* spp., suggesting that inoculants that are well-adapted to varieties and environmental conditions may have to be developed for maximum benefit of yields.

Mechanisms of nitrogen fixation by rhizobia

Nitrogen fixation happens through three different processes, including root hair penetration and infection thread formation, or rhizobia can infect their legume hosts and induce root or stem nodule formation (Liu et al., 2011). In some plants such as peanuts, where the infection process does not involve root hairs, the rhizobia can also enter the host through wounds or lateral root emergence (also known as “crack” entry) (Boogerd and Van Rossum, 1997; Ren, 2018); or penetration of root primordia found on the stem of some plants such as in *Sesbania* can result in entry (Froussart et al., 2016). But based on the information at hand, it appears that most species of legumes have their roots infected by rhizobia through root hair infection (Perrine-Walker et al., 2014; Wang et al., 2018). According to Lindström and Mousavi (2020), the *nod*, *nif* and *fix* genes dominantly regulate symbiotic nitrogen fixation in rhizobia. Additionally, other sets of genes in the bacteria regulate various aspects of the nodulation process (Hong et al., 2012). The “*nif*” genes which encode the nitrogen-fixing enzyme nitrogenase subunits and additional proteins required for nitrogenase synthesis, regulation, and function, and the “*nod*” genes, which encode proteins for Nod factor synthesis that induce various symbiotic responses on legume roots, are the main symbiosis genes being studied (Gopalakrishnan et al., 2015). According to Li et al. (2017), particular *nod* genes have been demonstrated to be important determinants of legume host specificity. Furthermore, Andrews and Andrews (2017) noted that because rhizobium strains are specialised, one rhizobium strain may infect some species of legumes but not others. The *nif* and *nod* genes, with the exception of *Bradyrhizobium*, are frequently carried on plasmids or symbiotic islands. These genes can be transferred (lateral transfer) between several bacterial species within a genus but seldom across genera (Shin et al., 2016).

The exchange of signals that enables mutual recognition and the activation of a signalling cascade is the first step in symbiotic interactions (Lindström and Mousavi, 2020). In reaction to the flavonoids released in plant root exudates, rhizobial lipochito-oligosaccharide signal molecules known as Nod factors are produced (Froussart et al., 2016). Nodule organogenesis begins when the plant detects the Nod factors. This is done by the root hair tips curling, which creates an infection thread, mitotic division of root cortical cells, and the formation of a nodule primordium (Rao, 2014). Thousands of living rhizobial symbionts, the majority of which are in the distorted form known as bacteroids, essentially colonise each root nodule (Ren, 2018). These bacteroids are encircled by membrane fragments from plant cells. N is fixed in these structures, known as symbiosomes-like structures, which may include numerous bacteroids or simply one (Babalola et al., 2017). Rhizobia differentiate into N₂-fixing bacteroids that use nitrogenase to catalyze the conversion of atmospheric N into ammonia (Mahmud et al., 2020; Jaiswal et al., 2021).

Rhizobia inoculation and its constraints

Various researchers have reported on the application of microbial consortia or single microbes as inoculum that could be employed in agriculture to remedy degrading soil conditions; however, the effective transfer of microbial inoculants from the lab to the field remains a challenge that requires urgent attention (Ahemad and Kibret, 2014; Pulido-Suárez et al., 2021). The transfer of microbial inoculants to the field is challenged by numerous factors such as crop species and crop variants, varying climatic conditions between fields, as well as by the exponential rise in the number of microbial isolates in recent years (Mfilinge et al., 2014; Ikenganyia et al., 2017).

According e.g. to Sajid et al. (2011); Singh et al. (2016), and Jaiswal and Dakora (2019), often regions regarded as geographic origins of legumes correlate with diversity hotspots of their respective symbionts. In addition, the performance of isolates on various local hosts varied, according to Grönemeyer et al. (2014), who found that most Namibian isolates were more effective in inducing nodulation on peanut and hyacinth bean grown in Namibia as opposed to the Angolan strains when used on the same varieties. Rhizobial strains frequently perform poorly in environments that are distinct from their original habitats, and Bünger et al. (2021) recently found that their efficacy depends on environmental parameters like soil temperature and soil texture, amongst others. Furthermore, Allito et al. (2020) suggested that soil pH and consequentially the amount of accessible phosphorus have sizable effects on inoculant success. However, Kanonge-Mafaune et al. (2018) pointed out that optimising the concentration of rhizobial cells per unit seed three times in cowpea and four times in beans has improved responses to inoculation and grain productivity. Comparing the usage of inoculants in consortia form to individual forms, Moreira et al. (2010) observed that the use of inoculant in consortia form increased growth of the woody legume species *Albizia lebbek* (L.) Benth, *Enterolobium contortisiliquum* (Vell.) Morong, and *Leucaena leucocephala*. It has also been discovered that seed coat compounds play a significant role in nodule development (Redjeki et al., 2013). This could be true as reported by Ibny et al. (2019) that variation in Bambara groundnut seed colour influences the choice of microsymbiont partners, through the attraction of native and familiar rhizobia with potential symbiotic efficiency within crop species.

Concluding remarks

It is anticipated that the adoption of contemporary technology will play a crucial part in the progress of the underutilised Bambara groundnut in the world and Africa in particular to increase production to feed the World's growing populations. Rhizobial inoculants are one way to boost the production of Bambara groundnut that need to be explored and developed for the benefit of the agricultural sector. There is also a need to develop better

strains of inoculants that suits the local environmental conditions and replace/solve the problem of exotic rhizobial strains whose survival rates in local soils are low due to severe and difference in the environmental and soil conditions. Since the Bambara is a native crop to Africa, an abundance of native rhizobia that are well adapted and capable of forming symbiotic relationships with the crop to efficiently fixing N may be available in local soils. It is suggested that temperature-resistant *Bradyrhizobium* strains should be isolated and selected on local soils (Grönemeyer and Reinhold-Hurek, 2018). Therefore, it is highly recommended for a comprehensive approach to the use of 'inoculants' and this should, include diagnostics of the field environment in relation to the desired crop. Furthermore, a holistic approach that investigate to determine the best agricultural practices, screening of available culture collections for inoculants, research in the area of microbiomes, and, integration of all the possible solutions into large-scale industrial production and field applications.

Author contributions

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

Funding

The German-Namibian cooperation was funded by grants of the Federal Ministry of Education and Research (BMBF, grant no. 01DG21008) and the German Academic Exchange Service (DAAD, grant no. 57558109) to BR-H and LNH in the framework of "Partnerships for sustainable solutions with Sub-Saharan Africa".

Conflict of interest

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2022.1004771/full#supplementary-material>

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