



Cultivation constrains of Bambara groundnut in Sub-Saharan Africa: Impact of Rhizobial Inoculants

Maria Lovisa Dhiginina Amwenyo ·
Lydia N. Horn · Thomas Hurek ·
Barbara Reinhold-Hurek · Abhijit Sarkar

Received: 13 November 2024 / Accepted: 23 December 2024 / Published online: 16 January 2025
© The Author(s) 2025

Abstract

Background The Sub-Saharan African food system is facing multiple threats, including soil nutrient depletion, monoculture cereal farming, population expansion, and climate change. These factors collectively pose a risk to agricultural productivity and food security in the region.

Scope Bambara groundnut (BGN) (*Vigna subterranea* [L.] Verdc) yield has been in decline due to various abiotic factors such as high temperature, drought, and salinity, as well as biotic factors like nitrogen-fixing symbiont host specificity. These challenges have negatively impacted crop productivity and food

security. This review highlights the significance of BGN in addressing food insecurity and explores its potential advantages for small-scale farmers. BGN provides a good example for strong effects of the microbiome, particularly specific symbionts for nitrogen-fixing root nodules, on production systems. A focus of this review is to highlight the potential applications of nitrogen-fixing symbionts as biofertilizers for Bambara groundnut.

Conclusion The review emphasizes the potential of BGN to improve agricultural production and soil fertility, particularly using inoculation technology, which could benefit small-scale farmers and contribute to enhancing food security. *Bradyrhizobium* inoculants may have to be designed specifically for the cultivar level of BGN.

Responsible Editor: Nabil Abrahi Hegazi.

M. L. D. Amwenyo
School of Agriculture and Fisheries Sciences, Faculty
of Agriculture, Engineering and Natural Resources,
University of Namibia, Ogongo Campus, P/Bag 5520,
Oshakati, Namibia

L. N. Horn
Zero Emissions Research Initiative, Multi-Disciplinary
Research Services, University of Namibia, 340 Mandume
Ndemufayo Avenue, P Bag 13301, Pionierspark,
Windhoek, Namibia

T. Hurek · B. Reinhold-Hurek (✉) · A. Sarkar
Faculty of Biology and Chemistry, Department
of Microbe-Plant Interactions, University of Bremen,
CBIB Center for Biomolecular Interactions Bremen, PO.
Box 330440, 28334 Bremen, Germany
e-mail: breinhold@uni-bremen.de

Keywords Bambara groundnut · *Vigna subterranea* · Food security · Nodulation · Inoculants · *Bradyrhizobium* · Soil fertility

Relevance of Bambara groundnut

Bambara groundnut (BGN) [*Vigna subterranea* (L.) Verdc] (BGN) is a drought-resistant, underutilized crop ranking third in significance of grain legumes after groundnut (Effa et al. 2019). It is a tropical legume crop that is native to sub-Saharan Africa and is a valuable source of food and income for many small-scale farmers in West and Central Africa. Along with

high nutritive value, BGN seeds possess gross energy value even larger than for other common pulses (Hillocks et al. 2012). BGN provides a balanced diet due to its high protein, carbohydrate, and fiber content, along with essential amino acids like lysine and methionine, which are more abundant than in cereals and other legumes. It is also a particularly rich source of magnesium, potassium, and iron compared to other pulses (Table 1). Apart from nutritional advantages, new and potential value-added uses of biologically active compounds in BGN as nutraceutical ingredients could be further investigated and exploited for various applications (Okafor et al. 2022).

BGN cultivation and hurdles

BGN production is one of the important practices among subsistence farmers in West African countries. In Southern Africa in Namibia, BGN gives promising yields even in areas with low rainfall and poor soil (Fig. 1). The optimal temperature for its growth ranges between 30–35 °C, with a minimum of 15 °C required for germination, and an annual rainfall of 600 to 750 mm (Hasan et al. 2018). The Africa-wide production of BGN has been recorded to be approximately 0.3 million tons annually, with Nigeria regarded as the largest producer of BGN in Africa at 0.1 million tons annually (Mayes et al. 2019). From 1999 to 2018, crop productivity in sub-Saharan Africa remained stagnant and low, ranging from 0.65 t ha⁻¹ to 0.78 t ha⁻¹ (Majola et al. 2021).

In spite of being a drought tolerant legume, BGN cultivation is still affected by climate change in several ways. Rising temperatures can lead to heat stress, reducing seed germination and plant growth, and negatively impact yields. Although resilient to drought, inconsistent rainfall can impair the germination or establishment of BGN seedlings in the early stages of crop growth. In Nigeria, drought and heat waves resulted in significant BGN crop losses in the recent years (Tyoakoso et al. 2019). Also, the photoperiod controls the yield and sink capacity of BGN (Kendabie et al. 2020). Moreover, the introduction of modern agriculture practices, such as the use of synthetic fertilizers and pesticides, have led to degradation of soil quality, making it difficult for BGN to grow (Babalola et al. 2017).

Changes in climate can alter traditional planting and harvesting dates, affecting local agricultural practices and food security. Warmer temperatures and changing humidity levels can create favorable conditions for pests and diseases, potentially leading to increased infestations and reduced crop health (Fatimah et al. 2022). Some of the major factors influencing BGN production in Namibia are insects, low yield, and use of unimproved land races (Valombola et al. 2021). BGN production can be seriously constrained by fungal pathogen *Macrophomina phaseolina* (Ouoba et al. 2019) and even the parasitic plant *Alectra vogelii* (yellow witchweed) (Musango et al. 2022). Lack of training for seed production, poor crop establishment, incorrect planting depth and plant spacing, use of unimproved seeds, low soil fertility, and a lack of effective nodulation technology all pose challenges to BGN production (Ikenganyia et al. 2017).

Symbiotic association of Bambara groundnut with *Bradyrhizobium*

Leguminous crops including BGN [*Vigna subterranea* (L.) Verdc] and cowpea (*Vigna unguiculata* L. Walp) are known for their ability to fix atmospheric nitrogen through root nodule symbioses with rhizobia (mainly *Bradyrhizobium* spp.) (Ajayi et al. 2020a). Although BGN is growing in marginal soils, with its promiscuous nodulation properties, it can create symbiotic association with different strains of soil bacteria of the genus *Bradyrhizobium* which exhibit varied compatibility and nitrogen fixation efficacy (Puozaa et al. 2017). For example, phylogenetically highly diverse *Bradyrhizobium* genospecies nodulate Bambara groundnut in Ghana (Adjei et al. 2022). The BGN nodule symbionts from Benin were even resistant against several abiotic stresses including high temperature, pH and NaCl (Zoundji et al. 2022). BGN may fix up to 200 kg N per ha (Ibny et al. 2019).

The nitrogen-fixing symbiosis with BGN has not only been shown to increase plant yield, but also to improve soil fertility (Yakubu et al. 2010). It is noted that BGN has a greater residual nitrogen effect than many other crops (Basu 2021): nitrogen fixed in nodules does not only benefit yield, but also decay of above-ground biomass and roots including nodules contribute organic and mineralized nitrogen to soils.

Table 1 Nutritional composition of examples of important grain legumes in comparison to Bambara groundnuts

	Bambara groundnut <i>Vigna subterranea</i>	Cowpea <i>Vigna unguiculata</i>	Chickpea <i>Cicer arietinum</i>	Green pea <i>Pisum sativum</i>	Lentil <i>Lens culinaris</i>	Lima Bean <i>Phaseolus lunatus</i>
Composition (g/100 g sample)						
Protein	18.8 ¹ / 19.6 ²	22 ³	19 ³	34 ⁴	31.4 ³	29 ⁵
Fat	1.4 / 5.5	1.6	6	2.4	1.2	5.3
Fibre	10.3 / 4.5	5.3	17	4.3	6.8	19
Ash	2.9 / 3.8	3.8	2.5	3.9	4.2	4.4
Carbohydrate	53 / 58	67 ⁷	60	55	57	57
Amino acids (g/100 g protein)						
Isoleucine	5.5 / 4.0	-	4.1	3.9 ³	9.6	5.3 ⁶
Leucine	10 / 7.5	4.4 – 10.6 ⁷	7.0	7.9	15.9	8.6
Lysine	8.0 / 6.5	5.4 – 7.5	7.7	6.3	12.6	7.2
Methionine	0.6 / 6.4 ⁷	1.2 – 2.2	1.6	1.6	1.6	1.2
Phenylalanine	7.7 / 5.5	NR	5.9	5.2	10.6	6.0
Threonine	4.4 / 3.5	3.0 – 5.0	3.6	4.5	7.6	4.6
Tryptophan	0.6 / 1.0	0.7 – 1.4	1.1	0.6	ND	ND
Valine	6.2 / 4.5	4.2 – 5.0	3.6	5.1	11.6	5.5
Arginine	7.5 / 7.0	4.5 – 8.5	10.3	7.9	14.0	5.5
Histidine	3.8 / 3.0	2.6 – 3.9	3.4	2.3	4.0	3.1
Alanine	5.1 / 4.0		4.4	4.8	39.8	4.6
Aspartic acid	14.6 / 10.0	8.8 – 16.9	11.4	11.2	26.1	11.8
Cysteine	2.4 /	0.5 – 0.5	1.3	0.4	0.4	ND
Glutamic acid	21 / 15.5	16.9 – 27.6	17.3	18.5	42.2	14.8
Glycine	4.5 / 4.0	NR	4.1	4.8	12.7	4.3
Proline	5.3 / 2.5	NR	4.6	4.6	11.4	4.6
Serine	6.9 / 5.5	NR	4.9	5.7	15.6	6.5
Tyrosine	3.1 / 2.5	NR	3.7	3.3	7.5	3.1
Minerals (g/100 g)						
Magnesium	136 / 125–555	184 ⁸	3.2–191 ⁷	86 ⁴	49 ⁴	149 ⁵
Potassium	NR / 308–2200	1112	994–1279	360	240	1340
Iron	8.8 / 11–150	8.2	4.5–53	10	8.5	5.7

¹ From reference (Yao et al. 2015); 10 samples of a landrace² From reference (Atoyebe et al. 2017); data from 20 different landraces³ From reference (Boye et al. 2010); a review; chickpea: Garbanzo beans⁴ From reference (El-Adawy et al. 2003); *Pisum sativum* variety Lencolen and *Lens culinaris* variety Giza 9⁵ From reference (Sahasakul et al. 2022); average of 10 varieties⁶ From reference (Evans and Boulter 1974); one varietal⁷ From reference (Halimi et al. 2019); a review⁸ From reference (Affrifah et al. 2022); a review

NR not reported

These increased N-pools in soil can benefit other crops grown in crop rotations. By adding nitrogen to the soil, this method lessens the demand for chemical fertilizers. With the exception of the fungivorous nematode abundance during the wet season, it has been observed that

the presence of legumes greatly enhanced also abundance and variety of soil biota (Gao et al. 2017).

Nitrogen-fixing legumes can also exert a positive effect in intercropping systems, where roots of the plants develop and die multiple times over their life



Fig. 1 Drought tolerant Bambara groundnut seedlings, growing at Mashare Agriculture Development Institute, Northern Namibia, three weeks without rain or irrigation

cycle, which causes the release of nitrogen through mineralization. In order to fully benefit from the potential of underutilized legumes for increased food security, there is a lack of knowledge on the mechanism of nutrient transfer between nodulating and non-nodulating plants. For example in Sorghum, grain yields increased when it was intercropped with pigeon pea as well as planted in legume residue (Gebremichael et al. 2019). In cassava-Bambara groundnut intercropping, more efficient land use and yield gain was observed depending on differences in the dates of sowing (Konan et al. 2023). In maize intercropping, among other legumes BGN produced considerable yields and increased the overall productivity of the cropping systems, and even reduced the plant parasite *Striga* (Oswald et al. 2002). This indicates that intercropping with legumes may have positive impact on farming, and it is beneficial to include legumes crops in management systems. Overall, also the symbiotic relationship between BGN and rhizobia is an important contributing factor to its success as a relevant crop in sub-Saharan Africa that needs to be explored to a greater extent.

Non-symbiotic interactions in BGN rhizosphere

Non-symbiotic interactions refer to interactions between plants and other organisms of the rhizosphere, a mutualistic relationship different from the symbiotic nodulation. Legumes generally produce

phenolics, which assist in pathogen activity declining, avail nutrients to plants, encourage the growth of beneficial microbes in the rhizosphere, and contribute to allelopathy (Weston and Mathesius 2013). Allelopathy occurs when plants release chemical compounds into the soil, which can influence the growth and development of neighboring plants (Weston and Mathesius 2013). Allelopathic compounds such as benzoxazinoids, which are known for inhibition of germination and growth of certain plant species, have been identified in BGN.

As in all plants, the rhizosphere of BGN is inhabited by a diverse community of microorganisms, including bacteria, fungi, and archaea which play a crucial role in nutrient cycling, plant and soil health. Recent research has shown that certain bacteria in the rhizosphere of BGN can solubilize phosphorus, making it more available for plant uptake (Olanrewaju and Babalola 2022). Plant growth promoting activity has also been reported from non-rhizobial nodule isolates of BGN from semi-arid regions of South Africa (Ayangbenro et al. 2023). Additionally, specific fungal species have been found to enhance the tolerance of BGN to abiotic stresses, such as drought and salinity (Gopalakrishnan et al. 2015). On the other hand, rhizobia may also serve as a promising source of plant growth-promoting molecules and interact with non-legume and other rhizobacteria (Fahde et al. 2023). Thus, learning more on non-symbiotic interactions in the BGN rhizosphere is important for sustainable agriculture and crop management.

The effects of rhizobia inoculant on BGN growth and yield

Rhizobia inoculation is an affordable effective and sustainable method for ensuring nitrogen supply in agronomic practices (Wilson et al. 2021). It is crucial for legumes in areas with low symbiont abundance. Tables 2 and 3 illustrate inoculant applications on BGN varieties in western sub-Saharan African countries (Table 2) and central, eastern and southern sub-Saharan countries (Table 3). The effects vary depending on strains, environmental conditions, and plant genotype. Peat-based inoculants, known for their security, longevity, and effectiveness, were commonly used to inoculate seeds (Fig. 2A). This often reduces the time of germination of BGN varieties in contrast

to non-inoculated ones as well as the time to reach to flowering (Sarkar et al. 2023). In field studies, *Bradyrhizobium* inoculant strains enhanced growth, biomass production and reduced the flowering days in BGN plants compared to nitrogen fertilizers (Ikenganyia et al. 2017). Also plant height and leaf numbers of certain BGN varieties were significantly improved by inoculation (Zoundji et al. 2024). Moreover, seeds obtained from BGN with inoculant treatment had less moisture contents which might facilitate longer shelf life and preservation time (Ajayi et al. 2024).

Furthermore, combining superphosphate and inoculants improved plant growth and root development, leading to increased nodule formation (Fig. 2B) (Mukakalisa 2010). Inoculants can be applied in different ways; however, the most common procedures include seed treatments, soil treatments, and root dipping into bacteria in suspension before or during planting. While soil-applied rhizobacterial inoculants increased BGN dry weight by 19%–25% compared to seed-applied inoculants, seed application remained cost-effective and effective for productivity improvement (Ikenganyia et al. 2017). Overall inoculant strains could effectively colonize the plant roots, leading to the formation of larger and more numerous nodules improving nitrogen availability producing more biomass than non-inoculated plants, as mentioned in Tables 2 and 3 (Bitire et al. 2022; 2023a; Bitire et al. 2023b; Gomoung et al. 2017; Hassen et al. 2023). It is therefore suggested that inoculation with highly effective strains is feasible and provides an environmentally friendly approach for enhancing grain yield in legumes (Gerrano et al. 2021; Konan et al. 2023) (see also Tables 2, 3). Moreover, also seeds quality such as hydration coefficient and cookability of cowpea can be positively affected by inoculating plants with specific *Bradyrhizobium* strains (Musa et al. 2011). Certain *Bradyrhizobium* strains were even found to exhibit antagonistic effects against fungal diseases, lowering disease incidence and improving plant health (Kebede 2021; Volpiano et al. 2019). On the other hand, inoculating BGN with Arbuscular Mycorrhizal Fungi (AMF), either amended with poultry manure or with Mulch could enhance leaf nutrient composition (Uko et al. 2020) or nodulation and root weight (Odoh et al. 2017), respectively, as mentioned in Table 2. More nitrogen and phosphorus were retained in the shoots of BGN when co-inoculated with *B. japonicum* and strain of

mycorrhiza *Glomus mossea* yielding higher plant biomass (Table 2) (Ajayi et al. 2020b). Thus, the phenomenon of rhizobial inoculation (either individual or co-inoculation) has gained attention because of its rising contribution to agricultural output. Furthermore, the combination of superphosphate and inoculants was reported to have positive effect on the plant growth and root development which led to nodule formation increment (Omari et al. 2022). Apart from symbionts, low-cost microbial inoculants of other beneficial microbes can aid in plant development, heavy metal contamination reduction, and phytopathogen management, all of which contribute to more sustainable agriculture (Fasusi et al. 2021).

Host-microbe specificity is common in many legumes and plays a key role in the spread of indigenous rhizobia and inoculant development. Factors influencing host specificity include variations in bacterial nodulation genes, surface polysaccharides such as exopolysaccharides and lipopolysaccharides, and plant signaling responses. BGN exhibits promiscuous nodulation with multiple rhizobial species, particularly from the cowpea miscellany group (Hassen et al. 2023). Cross-inoculation with symbionts originating from other legume species has been shown to improve nodule number, efficiency, and dry weight in several legumes, including BGN, in field trials across Guinea-savannah and Sudanian zones (Doloum et al. 2017). Also in Chad, cowpea cross-inoculant group isolates enhanced BGN growth and yield (Gomoung et al. 2017).

Challenges for BGN inoculation strategies

It was recognized already 30 years ago (Heller et al. 1997), that tremendous differences occur in the symbiotic efficacy of native bradyrhizobia which nodulate BGN: considerable variation in farm yields of BGN in Africa are common (600–3000 kg/ha) (Rachie and Silvestre 1977), and high-yielding cultivars from one country can perform poorly in another (Council 1979). It is therefore consequential that research on symbiotic effectiveness is regarded as a way to yield improvements in African BGN production (Heller et al. 1997).

Factors like soil type directly affect bacterial distribution and survival in soil, in turn affect legume nodulation, nitrogenase activity, and thus N₂

Table 2 Inoculant application on Bambara groundnut varieties across several western sub-Saharan African countries

Tested inoculant strains	Source of inoculant(s)	Host plant/BGN accessions/variety	Country	Inoculant application	Growing condition: pot or field experiment	Maximum yield or benefit	Reference
<i>Bradyrhizobium japonicum</i> strains FA3, RACA6, USDA110, and IRJ2180A	Indigenous rhizobia from the soil in both locations and seasons trapped by growing BGN	10 BGN accessions: TVSu-378, TVSu-506, TVSu-787, TVSu-1606, TVSu-1698, TVSu-1739, TVSu-710, TVSu-365, TVSu-475, and TVSu-305	Nigeria	BGN seeds coated with Arabic gum	Field experiment	RACA6 significantly enhanced the yield and yield component of TVSu-1698 than other inoculated BGN accessions with a mean value of $6,234 \pm 87$ kg ha ⁻¹	Bitire et al. 2023a
<i>Bradyrhizobium japonicum</i> strains FA3, RACA6, USDA110, and IRJ2180A	Indigenous rhizobia from the soil in both locations and seasons trapped by growing BGN	TVSu-378, TVSu-506, TVSu-787, TVSu-1606, TVSu-1698, TVSu-1739, TVSu-710, TVSu-365, TVSu-475, and TVSu-305	Nigeria	As broth to BGN seedlings	a) Pot experiment in glass houses b) Field experiment	Higher nodule numbers and weight in TVSu-1739 and TVSu-475 in both locations and seasons; highest nitrogen fixed values for genotypes TVSu-1739, TVSu-1698, TVSu-787, TVSu-365, TVSu-305, TVSu-710, and TVSu-1606, with a range of (62–67 kg ha ⁻¹), mostly enhanced by RACA6 and USDA110	Bitire et al. 2023b
<i>Bradyrhizobium yuandini</i> (indigenous)	Root nodules of BGN from pots in the plant house of SARI	purple variety	Ghana	As broth to BGN seedlings	Pot experiment in greenhouse having sterile river sand	2CL: highest nodulation, nodule dry weight, performing significantly more than the commercial strains, BR3267 and NC92, used as reference	(Imoro et al. 2023)
Unidentified genus and species; 14 strains: RVC1-14	Nodule isolates from three varieties of BGN: Ci5, Ci2 et Ci1 in the experimental fields	Red variety Ci5	Côte d'Ivoire	As broth to 14 days old BGN seedlings	Field experiment	Strains RVC8, RVC13 and RVC14 most effective and infective than the reference strain <i>S. meliloti</i> , yield of the BGN (number and weight of pods) much improved by strains RVC1, RVC4, RVC8, RVC13 and RVC14 compared to reference strain <i>S. meliloti</i>	(Guei et al. 2019)
<i>R. puseense</i> strain K39, <i>Rhizobium</i> sp. strains O12, T65 and un-identified strain O41	Trapping with soil from BGN agricultural fields in plastic bags	Local landrace with cream-colored red spotted seeds	Côte d'Ivoire	Post germinated seedlings of BGN inoculated with broth	In sterile sand contained in jars	Except for strain K39 others could well modulate the BGN land race	(Gnangui et al. 2019)

Table 2 (continued)

Tested inoculant strains	Source of inoculant(s)	Host plant/BGN accessions/variety	Country	Inoculant application	Growing condition: pot or field experiment	Maximum yield or benefit	Reference
Rhizobacteria inoculant	Nodumax legume inoculant manufactured by IITA business incubation platform, Ibadan Nigeria	Cultivar TVSU 1061 from IITA, Ibadan	Nigeria	a) 100 g nodumax inoculant (with gum Arabic sticker) slurry added to seeds, covered for 10 min to avoid direct sunlight, and then planted into moist seed bed or b) Rhizobial inoculants directly in planting holes of seed bed and then the uninoculated BGN seeds	Field studies	Soil inoculation rather than direct seed application of exogenous rhizobacteria and up to 75 kg P ha ⁻¹ enhanced the dry matter yield of and increased the postharvest soil total nitrogen content significantly	(Ikenganyia et al. 2017)
Rhizobia inoculant (Nodumax legume inoculant manufactured by IITA business incubation platform)	Commercial	BGN seeds (cultivar TVSU 1061) from IITA Ibadan	Nigeria	As liquid inoculum directly on the seeds at the sowing time by mixing with gum Arabic as sticker or directly by Soil inoculation at the planted holes on seed bed and then sowing seeds	Field study	Combined use of soil applied method of inoculation and planting 30 min after inoculation is highly recommendable	(Ikenganyia et al. 2018)
Inoculation with pre-made inoculums of four species of Arbuscular Mycorrhizal Fungi (AMF): <i>Glomus mosseae</i> , <i>Glomus deserticola</i> , <i>Glomus clarum</i> and <i>Gigaspora gigantea</i>	Inocula prepared from the starter cultures of arbuscular mycorrhizal fungi obtained from the Soil Microbiology Unit of the Department of Agronomy, University of Ibadan, Nigeria	BGN landrace -TVU 1729 from International Institute for Tropical Agriculture (IITA),	Nigeria	Poultry manure was applied at four rates of 0, 4, 8 and 12 t ha ⁻¹ and incorporated into the soil one week before planting whereas planting holes were partially filled with 30 g inoculum of each AMF according to specification	Field study in plots: Two seeds of BGN sown per hole and later thinned to one plant per stand two weeks after emergence	Soil inoculated with AMF inoculum and amended with 8- and 12-tons ha ⁻¹ of poultry manure in single or combination: more efficient and consistent in growth enhancement	(Uko et al. 2020)
Single or dual inoculation of <i>B. japonicum</i> USDA 110 and strain of mycorrhiza (<i>Glomus mosseae</i>)	Commercial	BGN	Ibadan, Nigeria	Inoculated with 1 ml of <i>B. japonicum</i> USDA 110 strain (109 cfu/ml), Mycorrhizal was applied to the plants 10 g, and 20 g (90 spores/g) at one week of growth and water applied at 10 ml, 20 ml and 50 ml every other day	screen house conditions in pots	More nitrogen and phosphorus were retained in the shoot of plants co-inoculated with <i>B. japonicum</i> and 20 g <i>G. mosseae</i> with higher biomass	(Ajayi et al. 2020b)
Arbuscular mycorrhizal fungal inoculum <i>Glomus mosseae</i> (with and without inoculum) and leguminous mulch (mulched and unmulched) treatments	Mycorrhizal inoculum collected from University of Ibadan. Leguminous mulch materials were air dried <i>Calopogonium mucunoides</i> shoots	3 varieties of BGN: TVSu 460, TVSu 617 and TVSu 622	Côte d'Ivoire, central Nigeria	Mycorrhizal inoculum: 10 g per pot; Mulch: 100 g per pot. All treatments were applied at 2 weeks after planting	Pot study with soil collected randomly from the farm as composite sample	The combined application of mulch and AMF increased the fresh root weight for all varieties from 10.3 –62.5%. AMF inoculation significantly increased the nodulation and root weight of TVSu 617 and TVSu 622	(Odoh et al. 2017)

Table 3 Inoculant application on Bambara groundnut varieties in several central, eastern and southern sub-Saharan African countries

Tested inoculant strains	Source of inoculant(s)	Host plant BGN accessions/variety	Country	Inoculant application	Growing condition: pot or field experiment	Maximum yield or benefit	Reference
<i>Bradyrhizobium elkanii</i> WBI, XBD5, <i>B. centrosema</i> XS34, <i>B. zhanggangense</i> XBD2, <i>Rhizobium tropici</i> UD5	Nodule isolates from <i>Glycine max</i> , <i>Desmodium uncinatum</i> , <i>Arachis hypogaea</i> , <i>Cynopsis tetragonoloba</i> and <i>Phaseolus vulgaris</i> respectively	Varieties: ZR S3, ZR S4, SB 11-1C, SB4-4G, BB4-4H, S1 Sel 2, Caprivi Sel 1, SB8-1B, S1 Sel 1, SB 14-7B, MV 67-1, MV 51-5-1C	South Africa	As broth on seeds	Leonard jars in Glass-house	Cross inoculants <i>B. zhanggangense</i> (XBD2) and <i>B. centrosema</i> (XS34): highest nodulation compatibility (nodule number and nodule dry weight with one or more BGN landraces	(Hassen et al. 2023)
GR: Groundnut Rhizobia, CR: Cowpea Rhizobia, SR: Soybean Rhizobia, BR: Bambara groundnut Rhizobia, MR: mélange des quatre Rhizobia	Rhizobium strains were produced from BGN, groundnut, cowpea, and soybean root nodules as cross inoculants at (ITRAD)	Local Djar variety	Chad, Cameroon	As liquid inoculum on seeds	Field experiment	Cross-inoculation: improvement of growth (plant sizes and biomasses) and seed yield at harvest: 491.25—910.375 kg•ha ⁻¹ (Chad); 327.26—699.77 kg•ha ⁻¹ (Cameroon). The enhanced yield expressed in kg/ha varied from 9.83% to 72.71%	(Gomoung et al. 2017)
Groundnut Rhizobium (GR); Cowpea Rhizobium (CR); Soybean Rhizobium (SR); BGN Rhizobium (BR)	Cross inoculant(s) for BGN produced from fresh nodule isolates from host plants groundnut, cowpea, or soybean, respectively by ITRAD Chad	Local variety Djar	Ngaoundere-Cameroon; Sudanian (Sarth-Chad)	As liquid inoculum on the seeds at the sowing time by mixing with milk Nido powder	Field experiment	BR: most successful inoculum for BGN, cowpea, and groundnut at Ngaoundere, whereas at Sarth, BR could be used to boost nodulation of BGN, soybean, and groundnut	(Doloum et al. 2017)
20 best performing isolates of indigenous rhizobia: Gram (-) and fast growers	BGN nodules from agricultural fields	Varieties: Azigokouiwéwé, Azigokouiwéwékpè	Sudan	As broth around the pregerminated inoculated seedlings	Pot experiments with local soil	Isolates resistant to various abiotic stress and yielded higher shoot dry weight and N uptake in a variety dependent manner	(Zoundji et al. 2022)
75 test isolates: closely related to type strains of <i>Bradyrhizobium arachidis</i> , <i>B. manausense</i> , <i>B. guangdongense</i> , <i>B. elkanii</i> , and <i>B. pacyrhizitzi</i> or even species yet to be characterized	Root nodules from 7 landraces (Local Variety, UNISWA Red, OM1, AS 17, SSD5, SSD8, and SSD9) were used as trap host in the field at the Malkerns Research station in the Middleveld and Luve sub-station in the Lower Middleveld	Red seed coated BGN landrace	Eswatini (formerly Swasiland)	Post germinated seedlings of BGN inoculated with broth	In sterile sand contained in sterile plastic pot in in a naturally lit glass-house	51% isolates more effective than the commercial strain, with relative symbiotic effectiveness ranging from 138 to 308%	(Dlamini et al. 2021)

Table 3 (continued)

Tested inoculant strains	Source of inoculant(s)	Host plant BGN accessions/variety	Country	Inoculant application	Growing condition: pot or field experiment	Maximum yield or benefit	Reference
89 isolates: <i>B. vignae</i> , <i>B. kavan-gense</i> , <i>B. subterraneum</i> , <i>B. elkanii</i> and <i>B. pachyrhizi</i> related	BGN nodules from farmers' fields in Mali, from experimental plots in Ghana and Googo as well as from South Africa	BGN landrace Uniswa red	South Africa	Post germinated seedlings of BGN inoculated with broth	In sterilized plastic pots containing auto-claved sand grown in glass-house and left to grow under natural conditions	Induced variable nodulation (nodule number and nodule dry matter) on their homologous host and varied in their N ₂ -fixing effectiveness	(Ibny et al. 2019)
<i>Bradyrhizobium</i> spp strains BAM-Kis1, BAMKis8, BAMKis4 and BAMKar3, <i>Burkholderia</i> spp strains BAMKbay8 and BAMsp3	18 nodulate isolates from Soil samples collected from farmers' fields in Port Victoria, Kisumu, Kendu bay, and Karungu	Kakamega Cream (KAKC) and Busia Brown (BUSB)	Kenya	As broth to BGN seedlings	Pot experiment in green-house	Seed treatment (some isolates): improved nodulation and plant growth; in some instances, outperforming the commercial strain <i>Bradyrhizobium japonicum</i> USDA110	(Benson and Fredrick 2019)
Various <i>Bacillus</i> isolates: <i>B. amyloliquefaciens</i> , <i>B. thuringiensis</i> , and <i>Bacillus</i> sp	Rhizobacteria from BGN soil samples as either biofertilizers or biocontrol agents or both	BGN seeds	South Africa	As broth on seeds before planting in freshly cultivated soil	Field study	<i>Bacillus</i> sp, <i>B. amyloliquefaciens</i> , <i>B. thuringiensis</i> , and control produced average of 41, 36, 25, and 20 seeds, respectively	(Ajillogba et al. 2022)



Fig. 2 Inoculant treatment of Bambara groundnut seeds before sowing in the field and formation of symbiotic root nodules at the time of harvest. Inoculation of Bambara groundnut seeds with an efficient *Bradyrhizobium* strain in a peat-based carrier

before planting (**A**), and symbiotic root nodules on Bambara groundnut roots at 60 days after germination (**B**) at Mashare Agriculture Development Center, Namibia, 2024

fixation (Sepp et al. 2023). Furthermore, factors such as climate, rainfall, and seasonality affect the distribution, diversity, and population density of *Bradyrhizobium* in African soils, influencing legume nodulation and nitrogen fixation, which in turn determines the critical need for inoculation (Grönemeyer and Reinhold-Hurek 2018). Effective rhizobia capable of nodulating a diverse range of host plants is required (Lindström et al. 2010). Furthermore, identifying indigenous rhizobia with a broader host range that are also resilient to abiotic stressors is critical for inoculant production, particularly in soils lacking effective indigenous rhizobia (Table 3) (Dlamini et al. 2021). Indigenous BGN-nodulating bacteria from different locations of Cameroon tolerant to some environmental stresses were better adapted to the respective soils than introduced inoculant strains (Laurette et al. 2015). Indeed, depending on the biome, inoculants can fail sometimes because foreign rhizobia compete poorly with indigenous rhizobia for nodule occupancy (Mendoza-Suárez et al. 2021). Ineffective or incompatible rhizobial strains as inoculant on the other hand, may result in diminished nodulation in BGN: The legume plant does not appear to be able to discriminate between effective and ineffective symbionts at the entry level (Westhoek et al. 2017). As a result, choosing the proper inoculant strain for BGN cultivation is critical for optimizing nodulation and nitrogen fixation.

This is further complicated by the high diversity land races of BGN with respect to grain types: seed coat pigmentation in BGN landraces, influenced by phenolic compounds, affects microsymbiont diversity and nodulation (Puozaa et al. 2021). Black seed coats appear to serve as markers for improved nodulation and N_2 fixation in South African landraces (Puozaa et al. 2021), while symbiont-plant interactions were found to vary significantly in BGN varieties from Namibia (Sarkar et al. 2023). In laboratory and greenhouse-pot studies using purified landraces of three divergent seed colors (cream, brown, and red), severe differences appeared to occur in different BGN race – symbiont combinations, regarding nodulation, agronomic traits and competitiveness of the strains (Sarkar et al. 2023). Such a pronounced plant genotype – symbiont genotype dependent response was also detected in field experiments for BGN. When 10 BGN accessions were combined with 4 different symbionts in Nigeria (Bitire et al. 2023a), some *Bradyrhizobium* strains even severely decreased the grain yield of certain cultivars over non-inoculated controls (e.g. strain USDA110 in TVSu-787, TVSu-1739 or TVSu-1606), while the same strain strongly increased yields in other cultivars (e.g. TVSu-710TVSu-305). Similar observations were made for other symbiont-BGN combinations in this study. Also in pot experiments using combinations of 12 South African land races and five bradyrhizobia, highly divergent shoot biomass responses were observed (Hassen et al. 2023). For example, strain XBQ5 decreased

or only slightly improved biomass compared to non-inoculated controls in races 34 and 42, while growth of race 38 was strongly elevated. The opposite responses were induced by strain XS34. Although it is tempting to speculate that responses may correlate with seed colors (races 34 and 42 have brown-, 38 cream-colored seeds), this was not consistent for other combinations in this study. Thus, more research is required on effective strain—plant genotype combinations. In contrast, in cowpea, different bradyrhizobial inoculant strains often do not show a preference for specific cowpea genotypes (Nyaga and Njeru 2020).

Conclusion

BGN, an underutilized African legume, could benefit from *Bradyrhizobium* inoculants to boost yields, though challenges arise from its symbiont promiscuity and genotype effects. Indigenous *Bradyrhizobium* strains, more effective and resilient than commercial ones and resistant to abiotic stresses, often have the potential to enhance plant performance and yield of BGN landraces. Developing inoculants from local strains for farmers could sustainably improve BGN growth and yield as well as soil fertility. More than in other grain legumes, in BGN effective nitrogen-fixing symbiotic interactions appear strongly dependent on specific plant-bacteria genotype combinations. This poses a challenge to develop inoculants for BGN, which may be further impeded by the prevalence of landraces over homozygous, well-characterized BGN cultivars. Thus, in modern breeding programs to elevate this underutilized legume to a modern crop, attention needs to be paid to select matching, efficient bacterial symbiont genotypes.

Acknowledgements The authors are grateful for funding of the German-Namibian cooperation. Grants of the Federal Ministry of Education and Research (BMBF, grant no. 01DG21008) and the German Academic Exchange Service (DAAD, grant no. 57558109) were given to BRH and LNH in the framework of “Partnerships for sustainable solutions with Sub-Saharan Africa”.

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

Funding Open Access funding enabled and organized by Projekt DEAL.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Adjei JA, Aserse AA, Yli-Halla M, Ahiabor BDK, Abaidoo RC, Lindstrom K (2022) Phylogenetically diverse *Bradyrhizobium* genospecies nodulate Bambara groundnut (*Vigna subterranea* L. Verdc) and soybean (*Glycine max* L. Merrill) in the northern savanna zones of Ghana. *FEMS Microbiol Ecol* 98. <https://doi.org/10.1093/femsec/fiac043>
- Affrifah NS, Philipps RD, Saalia FK (2022) Cowpeas: Nutritional profile, processing methods and products—A review. *Legume Sci* 4:e131. <https://doi.org/10.1002/leg3.131>
- Ajayi OO, Dianda M, Fagade OE (2020a) Evaluation of some nodulation genes found in Bambara symbiotic rhizobia strains. *J Microbiol Pathol* 5: 118. www.hilarispublisher.com/open-access/evaluation-of-some-nodulation-genes-found-in-bambara-symbiotic-rhizobia-strains.pdf
- Ajayi OO, Dianda M, Oyetunji OJ, Fabgola O, Fagade OE (2020b) Effects of combined inoculation of Bambara groundnut (*Vigna subterranea* L. Verdc.) with *Glomus mossae* and *Bradyrhizobium japonicum* on nitrogen and phosphorus uptake in shoot, plant biomass, leaf chlorophyll and mycorrhizal inoculation efficiency (MIE). *Fungal Terror* 3: 23–26. <https://doi.org/10.36547/ft.2020.3.3.23-26>
- Ajayi OO, Dianda M, Fagade OE (2024) Rhizobia inoculation's impact on the biomass and moisture content of leguminous Bambara groundnut (*Vigna subterranea* L. Verdc). *Discov Sustain* 5: 315. <https://doi.org/10.1007/s43621-024-00502-0>
- Ajillogba CF, Olanrewaju OS, Babalola OO (2022) Improving Bambara groundnut production: Insight into the role of omics and beneficial bacteria. *Front Plant Sci* 13. Art 836133. <https://doi.org/10.3389/Fpls.2022.836133>
- Atoyebi JO, Osilesi O, Adebawo O, Abberton M (2017) Evaluation of nutrient parameters of selected African accessions of Bambara groundnut (*Vigna subterranea*

- (L.) Verdc.) Am J Food Nutr 5: 83–89. <https://doi.org/10.12691/ajfn-5-3-1>.
- Ayanghenro AS, Adem MR, Babalola OO (2023) Bambara nut root-nodules bacteria from a semi-arid region of South Africa and their plant growth-promoting traits. Int J Microbiol 2023:218721. <https://doi.org/10.1155/2023/8218721>
- Babalola OO, Olanrewaju OS, Dias T, Ajilogba CF, Kutu FR, Cruz C (2017) Biological nitrogen fixation: The role of underutilized leguminous plants. In: D Panpatte, Y Jhala, R Vyas, H Shelat (eds) Microorganisms for green revolution: Microbes for sustainable crop production. Springer, Singapore. https://doi.org/10.1007/978-981-10-6241-4_20
- Basu MS (2021) Bambara groundnut: A promising food legume for dryland agriculture in India. Just Agric 2. <https://justagriculture.in/files/newsletter/2021/november/21.%20Bambara%20groundnut.pdf>
- Benson OO, Fredrick OO (2019) Assessment of rhizobia strains isolates of soils around Lake Victoria basin for their effectiveness in nodulation and symbiotic efficiency on soybeans and Bambara groundnuts. Int J Environ Agric Biotech 4:1469–1479. <https://doi.org/10.22161/ijeab.45.29>
- Bitire TD, Abberton M, Oyatomi O, Babalola OO (2022) Effect of *Bradyrhizobium japonicum* strains and inorganic nitrogen fertilizer on the growth and yield of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) accessions. Front Sustain Food Syst 6:913239. <https://doi.org/10.3389/fsufs.2022.913239>
- Bitire TD, Abberton M, Oyatomi O, Babalola OO (2023a) Yield response of accessions of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) inoculated with *Bradyrhizobium japonicum* strains. Front Sustain Food Syst 7:1142123. <https://doi.org/10.3389/fsufs.2023.1142123>
- Bitire TD, Abberton M, Tella EO, Edemodu A, Oyatomi O, Babalola OO (2023b) Impact of nitrogen-fixation bacteria on nitrogen-fixation efficiency of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) genotypes. Front Sustain Food Syst 14:1187250. <https://doi.org/10.3389/fsufs.2023.1187250>
- Boye J, Zare F, Pletch A (2010) Pulse proteins: Processing, characterization, functional properties and applications in food and feed. Food Res Int 43: 414–431. <https://doi.org/10.1016/j.foodres.2009.09.003>
- Council NR (1979) Tropical legumes: resources for the future. Academy of Sciences, Washington DC, USA
- Dlamini ST, Jaiswal SK, Mohammed M, Dakora FD (2021) Studies of phylogeny, symbiotic functioning and ecological traits of indigenous microsymbionts nodulating Bambara Groundnut (*Vigna subterranea* (L.) Verdc.) in Eswatini. Microb Ecol 82: 688–703. <https://doi.org/10.1007/s00248-021-01684-0>
- Doloum G, Ngakou A, Mbailao M (2017) Nodulation responses of four food crop legumes to cross-inoculation in the Guinea-savannah (Ngaoundere-Cameroon) and Sudanian (Sarh-Chad) zones. World J Agric Res 5: 117–125. <https://doi.org/10.12691/wjar-5-3-1>.
- Effa EB, Nwagwu F, Osai E (2019) Growth and yield response of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) to varying densities and phosphate fertilizer rates in Calabar, South Eastern Nigeria. Biology Agric Health Care 6:14–20. <https://iiste.org/Journals/index.php/JBAH/article/view/32511>
- El-Adawy TA, Rahma EH, El-Bedawey AA, E-Beltagy AE, (2003) Nutritional potential and functional properties of germinated mung bean, pea and lentil seeds. Plant Foods Hum Nutr 74:455–462. [https://doi.org/10.1016/S0308-8146\(01\)00163-7](https://doi.org/10.1016/S0308-8146(01)00163-7)
- Evans IM, Boulter D (1974) Amino-acid composition of seed meals of yam bean (*Sphenostylis stenocarpa*) and lima bean (*Phaseolus lunatus*). J Sci Food Agr 25: 919–922. <https://doi.org/10.1002/jsfa.2740250806>
- Fahde S, Boughribil S, Sijilmassi B, Amri A (2023) Rhizobia: A promising source of plant growth-promoting molecules and their non-legume interactions: Examining applications and mechanisms. Agr Ecosyst Environ 13:1279. <https://doi.org/10.3390/agriculture13071279>
- Fasusi OA, Cruz C, Babalola OO (2021) Agricultural sustainability: Microbial biofertilizers in rhizosphere management. Agriculture 11:163. <https://doi.org/10.3390/agriculture11020163>
- Fatimah S, Muafalah S, Nurholis N, Djunaed Ay (2022) Inventory of pests and diseases intensity on 10 Bambara groundnut (*Vigna subterranea* L. Verdc.) in the dryland of Madura during the dry season. Rekayasa 15:79–86. <https://doi.org/10.21107/rekayasa.v15i1.13988>
- Gao DD, Wang XL, Fu SL, Zhao J (2017) Legume plants enhance the resistance of soil to ecosystem disturbance. Front Plant Sci 8:1295. <https://doi.org/10.3389/fpls.2017.01295>
- Gebremichael A, Bekele B, Tadesse B (2019) Evaluation of the effect of sorghum-legume intercropping and its residual effect on yield of sorghum in yeki woreda, sheka zone, Ethiopia. Int J Agric Res Innov Technol 9:62–66. <https://doi.org/10.3329/ijar.v9i2.45412>
- Gerrano AS, Eifediyi EK, Labuschagne M, Ogedegbe FO, Hassen AI (2021) Production practices of Bambara groundnut. In: Oyeyinka, S.A., Ade-Omowaye, B.I.O. (eds) Food and potential industrial applications of Bambara groundnut, Springer Nature, Berlin. https://doi.org/10.1007/978-3-030-73920-1_2
- Gnangui SLE, Kouadjo CGZ, Zeze A (2019) First report of *Rhizobium pusense* within Voandzou (*Vigna subterranea* (L.) Verdc.) rhizosphere in Côte d'Ivoire. Microbiol Nat 1:55–65. <https://doi.org/10.26167/CZTB-1P42>
- Gomoung D, Mbailao M, Toukam ST, Ngakou A (2017) Influence of cross-inoculation on groundnut and Bambara groundnut- *Rhizobium* symbiosis: Contribution to plant growth and yield in the field at Sarh (Chad) and Ngaoundere (Cameroon). Am J Plant Sci 8:1953–1966. <https://doi.org/10.4236/ajps.2017.88131>
- Gopalakrishnan S, Sathya A, Vijayabharathi R, Varshney RK, Gowda CLL, Krishnamurthy L (2015) Plant growth promoting rhizobia: challenges and opportunities. 3 Biotech 5:355–377. <https://doi.org/10.1007/s13205-014-0241-x>
- Grönemeyer JL, Reinhold-Hurek B (2018) Diversity of bradyrhizobia in Subsahara Africa: A rich resource. Front Microbiol 9(2194):21. <https://doi.org/10.3389/fmicb.2018.02194>
- Guei NKR, Konate I, Bakayoko S, Ouattara A, Amani K, Tidou AS, Filali-Mltouf A (2019) Nodulation and

- agronomic performance of indigenous rhizobia isolated from Bambara groundnut (*Vigna subterranea* L.) nodules in Dalao, Côte d'Ivoire'. *Int J Res Stud Microbiol Biotechnol* 5:13–18. <https://doi.org/10.20431/2454-9428.0502004>
- Halimi RA, Barkla BJ, Mayes S, King GJ (2019) The potential of the underutilized pulse bambara groundnut (*Vigna subterranea* (L.) Verdc.) for nutritional food security. *J Food Comp Anal* 77:47–59. <https://doi.org/10.1016/j.jfca.2018.12.008>
- Hasan M, Uddin MK, Mohamed MTM, Zuan ATK (2018) Nitrogen and phosphorus management for Bambara groundnut (*Vigna subterranea*) production: A review. *Legume Res* 41:483–489. <https://doi.org/10.18805/Lr-379>
- Hassen AI, Bopape FL, van Vuuren A, Gerrano AS, Morey L (2023) Symbiotic interaction of bambara groundnut (*Vigna subterranea*) landraces with rhizobia spp. from other legume hosts reveals promiscuous nodulation. *South Afr J Bot* 160:493–503. <https://doi.org/10.1016/j.sajb.2023.07.032>
- Heller J, Begemann F, Mushonga J (1997) Bambara groundnut, *Vigna subterranea* (L.) Verdc. Promoting the conservation and use of underutilized and neglected crops n. 9. Leibniz Institute of Plant Genetics and Crop Plant Research; International Plant Genetic Resources Institute, Gatersleben (Germany), Rome (Italy). <https://hdl.handle.net/10568/104199>
- Hillocks RJ, Bennett C, Mponda OM (2012) Bambara nut: A review of utilisation, market potential and crop improvement. *Afr Crop Sci J* 20:1–16
- Ibny FYI, Jaiswal SK, Mohammed M, Dakora FD (2019) Symbiotic effectiveness and ecologically adaptive traits of native rhizobial symbionts of Bambara groundnut (*Vigna subterranea* L. Verdc.) in Africa and their relationship with phylogeny. *Sci Rep* 9:12666. <https://doi.org/10.1038/s41598-019-48944-1>
- Ikenganyia EE, Anikwe MAN, Ngwu OE (2017) Influence of rhizobacteria inoculant application methods and phosphate fertilizer rates on dry matter accumulation, yield of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) and soil total nitrogen content in a degraded ultisol in Southeast Nigeria. *Agrotechnol* 6:1000165. <https://doi.org/10.4172/2168-9881.1000165>
- Ikenganyia E, Anikwe MAN, Ngwu O (2018) Impacts of plant growth promoting rhizobacteria inoculation configurations on vegetative growth, nodulation and yield of Bambara groundnut [*Vigna subterranea* (L.) Verdc.]. *Int J Agric Biol* 2:54–69. <https://doi.org/10.22161/ijhaf.2.3.5>
- Imoro AWM, Pobee J, Akaband F (2023) Isolation of rhizobia from the nodules of Bambara groundnuts for inoculant production. *J Agricult Sci* 15:47–54. <https://doi.org/10.5539/jas.v15n4p47>
- Kebede E (2021) Competency of rhizobial inoculation in sustainable agricultural production and biocontrol of plant diseases. *Front Sustain Food Syst* 5:728014. <https://doi.org/10.3389/fsufs.2021.728014>
- Kendabie P, Jrgensen ST, Massawe F, Fernandez J, Azam-Ali S, Mayes S (2020) Photoperiod control of yield and sink capacity in Bambara groundnut (*Vigna subterranea*) genotypes. *Food Energy Secur* 9. ARTN e240. <https://doi.org/10.1002/fes3.240>
- Konan KM, Kouassi K, Bonny BS, Doubi BTS, Zoro BIA, Dogbo DO (2023) The efficiency of cassava-Bambara groundnut intercropping according to the sowing date of cassava. *S Afr J Plant Soil* 40:86–94. <https://doi.org/10.1080/02571862.2023.2206166>
- Laurette NN, Maxémilienne NB, Henri F, Souleymanou A, Kamdem K, Albert N, Dieudonné N, François-Xavier E (2015) Isolation and screening of indigenous Bambara groundnut (*Vigna subterranea*) nodulating bacteria for their tolerance to some environmental stresses. *Am J Microbiol Res* 3:65–75. <https://doi.org/10.12691/AJMR-3-2-5>
- Lindström K, Murwira M, Willems A, Altier N (2010) The biodiversity of beneficial microbe-host mutualism: The case of rhizobia. *Res Microbiol* 161:453–463. <https://doi.org/10.1016/j.resmic.2010.05.005>
- Majola NG, Gerrano AS, Shimelis H (2021) Bambara groundnut ([L.] Verdc.) production, utilisation and genetic improvement in Sub-Saharan Africa. *Agronomy-Basel* 11. ARTN 1345. <https://doi.org/10.3390/agronomy11071345>
- Mayes S, Ho WK, Chai HH, Gao XQ, Kundy AC, Mateva KI, Zahrulakmal M, Hahiree MKIM, Kendabie P, Licea LCS, Massawe F, Mabhaudhi T, Modi AT, Berchie JN, Amoah S, Faloye B, Abberton M, Olaniyi O, Azam-Ali SN (2019) Bambara groundnut: an exemplar underutilised legume for resilience under climate change. *Planta* 250:803–820. <https://doi.org/10.1007/s00425-019-03191-6>
- Mendoza-Suárez M, Andersen SU, Poole PS, Sánchez-Canizares C (2021) Competition, nodule occupancy, and persistence of inoculant strains: Key factors in the *Rhizobium-legume* symbioses. *Front Plant Sci* 12:690567. <https://doi.org/10.3389/fpls.2021.690567>
- Mukakalisa C (2010) Molecular, environmental and nutritional evaluation of Bambara groundnut (*Vigna subterranea* (L.) Verdc.) for food production in Namibia. University of Namibia, Windhoek.
- Musa ME, Elsheikh EAE, Ahmed IAM, Elfadil E, Babiker EE (2011) Effect of intercropping, *Bradyrhizobium* inoculation and N, P fertilizers on yields, physical and chemical quality of cowpea seeds. *Front Agric China* 5:543–551. <https://doi.org/10.1007/s11703-011-1147-6>
- Musango R, Pasipanodya JT, Tamado T, Mabasa S, Makaza W (2022) A threat to Bambara groundnut production under climate change: A review paper. *J Agric Chem Environ* 11:83–105. <https://doi.org/10.4236/jacen.2022.112006>
- Nyaga JW, Njeru EM (2020) Potential of native rhizobia to improve cowpea growth and production in semiarid regions of Kenya. *Front Agron* 2:606293. <https://doi.org/10.3389/fagro.2020.606293>
- Odoh NC, Idibia P, Ncho OC (2017) Varietal response of Bambara groundnut (*Vigna subterranea*) to mulching and AMF inoculation in central Niger. *J Advanc Agric* 7:1030–1035. <https://doi.org/10.24297/jaa.v7i2.6149>
- Okafor JNC, Jideani VA, Meyer M, Le Roes-Hill M (2022) Bioactive components in Bambara groundnut (*Vigna subterranea* (L.) Verdc) as a potential source of nutraceutical ingredients. *Heliyon* 8: e09024. ARTN e09024. <https://doi.org/10.1016/j.heliyon.2022.e09024>

- Olanrewaju OS, Babalola OO (2022) Plant growth-promoting rhizobacteria for orphan legume production: Focus on yield and disease resistance in Bambara groundnut. *Front Sustain Food Syst* 6:922156. <https://doi.org/10.3389/fsufs.2022.922156>
- Omari RA, Yuan K, Anh KT, Reckling M, Halwani M, Egamberdieva D, Ohkama-Ohtsu N, Bellingrath-Kimura SD (2022) Enhanced soybean productivity by inoculation with indigenous strains in agroecological conditions of Northeast Germany. *Front Plant Sci* 12:707080. <https://doi.org/10.3389/fpls.2021.707080>
- Oswald A, Ransom JK, Kroschel J, Sauerborn J (2002) Inter-cropping controls *Striga* in maize based farming systems. *Crop Prot* 21:367–374. [https://doi.org/10.1016/S0261-2194\(01\)00104-1](https://doi.org/10.1016/S0261-2194(01)00104-1)
- Ouoba A, Sawadogo N, Ouedraogo MH, Nandkangre H, Konate MN, Zida EP, Soalla RW, Ouédraogo M, Sawadogo M (2019) Phenotyping Bambara groundnut landraces for resistance to *Macrophomina phaseolina* (Tassi) Goidnich. *Int J Agric Biol* 21:547–552. <https://doi.org/10.17957/ijab/15.0927>
- Puozaa DK, Jaiswal SK, Dakora FD (2017) African origin of *Bradyrhizobium* populations nodulating Bambara groundnut (*Vigna subterranea* L. Verdc) in Ghanaian and South African soils. *PLoS One* 12: e0184943. <https://doi.org/10.1371/journal.pone.0184943>. PONE-D-17-06507 [pii]
- Puozaa DK, Jaiswal SK, Dakora FD (2021) Black seedcoat pigmentation is a marker for enhanced nodulation and N₂ fixation in Bambara Groundnut (*Vigna subterranea* L. Verdc.) landraces. *Front Agron* 3. ARTN 692238. <https://doi.org/10.3389/fagro.2021.692238>
- Rachie KO, Silvestre P (1977) Grain legumes. In: Leakey CL, Wills JB (eds) Food crops of the lowland tropics. Oxford University Press, London
- Sahasakul Y, Aursalung A, Thangsiri S, Wongchang P, Sangkasa-Ad P, Wongpia A, Polpanit A, Inthachai W, Temviriyankul P, Suttisansanee U (2022) Nutritional compositions, phenolic contents, and antioxidant potentials of ten original lineage beans in Thailand. *Foods* 11: 2064. <https://doi.org/10.3390/foods11142062>. ARTN 2062
- Sarkar A, Fwanyanga FM, Horn LN, Welzel S, Diederichs M, Kerk LJ, Zimmermann M, Reinhold-Hurek B (2023) Towards inoculant development for Bambara groundnut (*Vigna subterranea* (L.) Verdc) pulse crop production in Namibia. *Front Plant Sci* 14:1270356. <https://doi.org/10.3389/fpls.2023.1270356>
- Sepp SK, Vasar M, Davison J, Oja J, Anslan S, Al-Quraishi S, Bahram M, Bueno CG, Cantero JJ, Fabiano EC, Decocq G, Drenkhan R, Fraser L, Oriol RG, Hiiesalu I, Koorem K, Kõljalg U, Moora M, Mucina L, Öpik M, Polme S, Pärtel M, Phosri C, Semchenko M, Vahter T, Palacios AMV, Tedersoo L, Zobel M (2023) Global diversity and distribution of nitrogen-fixing bacteria in the soil. *Front Plant Sci* 14:1100235. <https://doi.org/10.3389/fpls.2023.1100235>
- Tyoakoso MM, Tougous MD, Babayola M (2019) Effects of nitrogen rate on growth and yield of Bambara groundnut (*Vigna subterranea* (L.) Verdc.). *Int J Res Granthaalayah* 7: 67–76. <https://doi.org/10.29121/granthaalayah.v7.i12.2019.301>
- Uko AE, Effa EB, Isong A, Effiong JE (2020) Yield performance and leaf nutrient composition of Bambara groundnut under arbuscular mycorrhizal inoculation in a poultry manure amended ultisol. *Pak J Biol Sci* 23:1397–1407. <https://doi.org/10.3923/pjbs.2020.1397.1407>
- Valombola JS, Awala SK, Hove K (2021) Farmers' preferences, seed source, production constraints and improvement needs assessment of Bambara Groundnut (*Vigna subterranea* [L.] Verdc.) in northern rural of Namibia. *Sci Papers, Ser Manag Econom Eng Agric Rural Dev* 21:789–797
- Volpiano CG, Lisboa BB, Granada CE, José JFBS, de Oliveira AMR, Beneduzi A, Perevalova Y, Passaglia LMP, Vargas LK (2019) Rhizobia for biological control of plant diseases. In: Kumar V, Prasad R, Kumr M, Choudhary DK (eds) Microbiome in plant health and disease: Challenges and opportunities. Springer, Singapore
- Westhoek A, Field E, Rehling F, Mulley G, Webb I, Poole PS, Turnbull LA (2017) Policing the legume-Rhizobium symbiosis: a critical test of partner choice. *Sci Rep* 7: 1419. <https://doi.org/10.1038/s41598-017-01634-2>. ARTN 1419
- Weston LA, Mathesius U (2013) Flavonoids: their structure, biosynthesis and role in the rhizosphere, including allelopathy. *J Chem Ecol* 39:283–297. <https://doi.org/10.1007/s10886-013-0248-5>
- Wilson G, Ulzen J, Abaidoo RC, Opoku A, Adjei-Nsiah S, Osei O (2021) Native rhizobia strains enhance seed yield of groundnut varieties in Northern Ghana. *Front Agron* 3:653044. <https://doi.org/10.3389/fagro.2021.653044>
- Yakubu H, Kwari JD, Ngala AL (2010) N₂ Fixation by grain legume varieties as affected by rhizobia inoculation in the sandy loam soil of sudano-sahelian zone of North Eastern Nigeria. *Nigerian J Bas Appl Sci* 18: 229–236. <http://ajol.info/index.php/njbas/index>
- Yao DN, Kouassi KN, Erba D, Scazzina F, Pellegrini N, Casiraghi MC (2015) Nutritive evaluation of the Bambara groundnut Ci12 landrace [*Vigna subterranea*(L.) Verdc. (*Fabaceae*)] produced in Cote d'Ivoire. *Int J Mol Sci* 16: 21428–21441. <https://doi.org/10.3390/ijms160921428>
- Zoundji MCC, Ahoglé AMA, Akplo TM, Gangnon SO, Montéiro D, Zanzo Y, Alladassi FK, Hounngandan P (2022) Resistance to abiotic stress and effectiveness of native rhizobia on Bambara groundnut [*Vigna subterranea* (L.) Verdc.] in Benin. *Open J Soil Sci* 12: 193–215. <https://doi.org/10.4236/ojss.2022.126008>
- Zoundji MCC, Tovizoukou SM, Akplo MT, Ahogle AMA, Balogoun I, Kouelo FA, Adandonon A, Hounngandan P (2024) Rhizobial biofertilizers and Bambara groundnut (*Vigna subterranea* L. Verdcourt) production: Unveiling the synergistic potential for growth and yield in Benin's challenging sub-humid zone. *Int J Biosci* 24: 138–150. <https://doi.org/10.12692/ijb/24.5.138-150>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.