

Full Length Research Paper

Inoculation effectiveness of native and exotic *Bradyrhizobium* species strains in a Senegalese agricultural soil: A comparison on modern and traditional peanut (*Arachis hypogaea* L.) cultivars

Godar Sene^{1,2*}, Nibourou Top^{1,2}, Maimouna Cissoko^{1,3}, Nogaye Niang^{1,2}, Cheikh Ndiaye^{1,2}, Issa Faye⁴, Mansour Thiao^{1,2}, Saliou Fall^{1,4} and Samba Ndao Sylla^{1,2}

¹Laboratoire Commun de Microbiologie (LCM) IRD/ISRA/UCAD, Centre de Recherche et de Formation à la Recherche IRD/ISRA de Bel-Air, BP 1386. CP 18524 Dakar, Sénégal.

²Département de Biologie végétale, Université Cheikh Anta Diop (UCAD), BP 5005, Dakar-Fann, Sénégal.

³Institut de Recherche pour le Développement-IRD, Hann Bel Air, Route des hydrocarbures - BP 1386 CP 18524 Dakar, Sénégal.

⁴Institut Sénégalais de Recherches Agricoles-ISRA, Hann Bel Air, Route des hydrocarbures - BP 3120 Dakar, Sénégal.

Received 3 September 2023; Accepted 8 November 2023

Peanut is a key component of Senegal's predominantly cereal-based farming systems, but its production is challenged by low soil fertility. Rhizobial inoculation is a promising strategy to improve crop yield and reduce the use of chemical nitrogen fertilizers. The aim of this study was to isolate the most specific and effective bradyrhizobial strain for peanut, and to determine the degree of variability in the response of peanut cultivars to inoculation. The seeds of five cultivars: *55-437*, *Fleur 11*, *Sunu Gaal*, *Amoul Morom* and *Essamaay* were inoculated individually with ten bradyrhizobial strains (LMG9283 and USDA3187, which are the reference strains; ISRA400, ISRA453, ISRA454, ISRA519, ISRA534 and ISRA538, isolated from *Fleur 11* in Senegal, and ORS3640 and ORS3644, isolated from herbaceous species that are commonly found in Senegalese farmers' fields). The plants were grown under greenhouse conditions in a mixture of sandy soil and vermiculite (1/1, v/v). The results obtained in terms of nodule formation, plant growth and yield parameters showed a positive effect of bradyrhizobial inoculation. However, these data indicated that the response of peanut to inoculation was cultivar dependent, with the traditional cultivars *55-437* and *Fleur 11* showing the greatest increase in plant growth and yield parameters. Our results also highlighted the need for cultivar-specific selection of *Bradyrhizobium* to improve inoculation success in peanut, with the indigenous isolates being specifically more effective than the reference strains. According to this study, it would be beneficial to promote the use of native isolates that perform well with the peanut cultivars studied.

Key words: Peanut (*Arachis hypogaea*), inoculation, indigenous and exotic *Bradyrhizobium* strains, nodulation, growth, yield parameters.

INTRODUCTION

The peanut, also known as groundnut (*Arachis hypogaea* L.), is an important grain legume grown in the tropics and

subtropics, including sub-Saharan Africa, and consumed worldwide for human and animal feeding (Noba et al., 2014). In Senegal, peanut has been a cash crop for over a century, contributing to 60% of the country's agricultural gross domestic product and approximately 80% of its export earnings (Sene et al., 2010; Noba et al., 2014). It is the main oil-producing crop and the four oil factories established in the country formed the backbone of the national industrial fabric. After a long period of decline, peanut yields have increased in the last five years. However, the factors that determine these increases, that is, soil fertility, have steadily deteriorated, with a reduction in fallow land and low levels of fertilizer use (Sene et al., 2010, 2023). Various agricultural practices, including the use of urea, have been adopted to boost yields and mitigate food shortages. However, the high cost of chemical nitrogen fertilizer and the necessity for sustainable alternative sources has increased the strategic importance of microbial inoculation.

Microbial inoculation is a promising strategy to improve crop yields and minimize dependence on chemical fertilizers, thereby fostering environmentally friendly agriculture (Kahindi et al., 1997; Garg et al., 2018; Itelima et al., 2018; Sene et al., 2023). Among these microbial communities, soil bacteria, collectively referred to as rhizobia, hold a pivotal role in improving crop production (Giller, 2001). The demand for rhizobial inoculants is therefore growing, driven by the need for sustainable and environmentally friendly agricultural practices and safer and healthier food (Lesueur et al., 2016; Mohanty and Swain, 2018; Sene et al., 2021, 2023).

Rhizobia are symbiotic bacteria that induce the formation of new organs called nodules on the roots of certain legume hosts, within which the bacteria multiply, differentiate into bacteroids and subsequently convert the atmospheric nitrogen into ammonia (Peoples et al., 1995; Kahindi et al., 1997; Giller, 2001). The rhizobia-legume symbiosis is one of the most important nitrogen-fixing systems (Kahindi et al., 1997). The isolation and selection of elite rhizobial strains is very important because the effective rhizobial strains can be used as inoculants for effective nodulation (Dudeja and Khurana, 1988; Dhery and Dreyfus, 1991; Lanier et al., 2005; Bogino et al., 2006; Zaiya et al., 2018). Inoculation can provide sufficient numbers of viable and effective rhizobia to facilitate rapid root nodulation and ultimately to achieve optimum yields. Rhizobial inoculants offer an alternative to industrial nitrogen fertilizers and a means of preserving or improving soil fertility (Peoples et al., 1995; Alves et al., 2003; Chalk et al., 2006). Despite their potential, the commercialization of microbial inoculants has lagged behind the expectations in West Africa, and successful establishment of legume crops in these countries

requires an effective symbiotic association between elite strains and compatible host plants (Lesueur et al., 2016). Like many other legumes, peanut has the ability to form a mutualistic symbiosis with rhizobia. For this symbiosis to be successful, there must be a sufficient quantity of fresh, vigorous bacteria ready to enter the roots and multiply rapidly. This symbiotic partnership serves as the most efficient and effective method of supplying nitrogen to the leguminous crops, especially when the soil is void of the specific rhizobial agents. In Senegal, peanut is so far considered to be nodulated by the genus *Bradyrhizobium* (Sene et al., 2010; Zaiya et al., 2018), the so-called slow-growing rhizobia. However, selected bradyrhizobial strains often fail to compete with indigenous soil rhizobia in Senegalese soils and do not increase nodulation. Their competitive ability is an important factor in determining their success (Sene et al., 2010). Furthermore, some authors reported that modern high-yielding and traditional cultivars differ in their response to microbial inoculation (Chen et al., 2003; Meghvansi et al., 2008; Argaw, 2017). This suggests the need for cultivar-specific rhizobial selection prior to inoculum formulation. Therefore, the present study was undertaken to isolate the most specific and effective *Bradyrhizobium* species inoculants for five modern and traditional Senegalese peanut cultivars and to use elite strains as inoculants. Our hypothesis asserts that the peanut's response to rhizobial inoculation would vary between cultivars and that this variability would differ between modern and traditional cultivars.

MATERIALS AND METHODS

Plant

Five local peanut (*A. hypogaea* L.) cultivars kindly obtained from the Centre National de Recherche Agronomique (CNRA) in Bambey, Senegal, were used in this experiment. These cultivars were selected on the basis of the taste desired by the local population and their characteristics shown in Table 1.

Bradyrhizobial materials

The bradyrhizobial strains used in this study are from the collection of the Laboratoire Commun de Microbiologie (LCM) IRD/ISRA/UCAD, Dakar, Senegal. Six of them (ISRA 400, ISRA453, ISRA454, ISRA519, ISRA534 and ISRA538) are indigenous bradyrhizobia isolated from the peanut cultivar *Fleur 11* grown in soils sampled from the Senegalese peanut production basin (Zaiya et al., 2018). The two strains ORS3640 and ORS3644 are also indigenous and were isolated from herbaceous species that coexist with peanut crops (Sene et al., 2012, 2013). In this experiment, they were tested against two reference bradyrhizobial strains (USDA3187 and LMG9283) (Castro et al., 1999; Sene et al., 2010).

*Corresponding author. E-mail: godar.sene@ucad.edu.sn. ORCID ID: 0000-0001-8434-019X.

Table 1. Characteristics of the peanut cultivars used in the study.

Cultivar	Type	Growth habit	Growth cycle (days)	Registration in Senegal
<i>Fleur 11</i>	Spanish	Erect	90	Traditional, since 1955
55-437	Spanish	Erect	90	Traditional, since 1993
<i>Sunu Gaal</i>	Spanish	Erect	95	New, since 2017
<i>Essamay</i>	Virginia	Semi-erect	105	New, since 2017
<i>Amoul Morom</i>	Virginia	Semi-erect	120	New, since 2017

Greenhouse experimental design

The experiment was set up in the greenhouse (Bel Air Experimental Station, 14°44'N, 17°30'W in Dakar) using a non-sterile soil from Sangalkam, 30 km east of Dakar mixed with sterilized vermiculite at 120°C for 20 min (1:1, v/v). This soil has a pH of 6.5 with 58.15, 32.8 and 3.6% of sand, loam and clay, respectively and contains 0.06% total nitrogen (N), 0.54% total carbon (C), 39 mg phosphorus (P) kg⁻¹ total P, 4.8 mg P kg⁻¹ available P. It was sieved (< 1 mm), homogenized and used to fill up the pots. Seeds of selected cultivars (Table 1) of peanut were first surface sterilized (to avoid seed-borne diseases) with 5% sodium hypochlorite (NaOCl) for 5 min, 70% ethanol for 3 min and thoroughly rinsed with sterile distilled water. The seeds were then placed on Petri dishes containing moist filter paper for germination under sterile conditions and kept in the dark at 25°C. The germinated seeds were manually transplanted into 1.5 L plastic pots disinfected with a solution containing 1.81% of calcium hypochlorite and filled with the substrate to a depth of 2 to 3 cm. Two germinated seeds were planted in each pot. The plants were thinned on the 3rd day after planting to one plant per pot. The pots were arranged in randomized blocks, with a single inoculation and five replications. The pots were placed at 10 and 40 cm spacing within and between rows for the cultivars *Fleur 11*, *55-437* and *Sunu Gaal*. The distance between the pots was 10 and 60 cm for the cultivars *Amoul Morom* and *Essamay*. The plants were grown for 65 days under greenhouse conditions (temperature of 27-35°C, relative humidity of 70-80% and 12 h of light) and were watered every two days with chlorine treated tap water without added nutrients.

Inoculant preparation and inoculation

The greenhouse experiment consisted of 11 treatments: eight with application of indigenous bradyrhizobial inoculants compared with two reference strains, and a negative control without inoculation for each cultivar. The inoculants were prepared as follows: each *Bradyrhizobium* strain was grown in 250 mL Erlenmeyer flasks containing 100 mL yeast extract-mannitol (YEM) medium (Vincent, 1970) for 3 days at 28°C with rotary shaking at 150 rpm. Five milliliters (containing 10⁸ cells mL⁻¹) of the bacterial culture at its logarithmic growth stage were used to inoculate the plants. The inoculants were applied directly to the soil surface at the base of the stem five days after emergence to ensure that the bacteria reached the roots. Treatments without bradyrhizobial inoculum received 5 mL of autoclaved inoculum in order to avoid differences in soil nutrient content associated with the addition of rhizobial inoculum.

Collection of growth and yield variables

Data on growth variables (plant height and number of branches) and leaf chlorophyll content for each cultivar were collected at flowering [30 days after planting (DAP)], pod filling (45 DAP) and pod maturity periods (60 DAP). Plant height (cm) was measured with a ruler from the base of the stem to the apex, while the number

of branches was counted manually. Leaf chlorophyll content was estimated at 30, 45 and 65 DAP using a SPAD-502Plus chlorophyll meter (Konica-Minolta). At harvest, whole peanut plants were uprooted. The soil adhering to the roots was removed under running tap water and the nodules were picked and counted. The pods were manually stripped from the plants to record the yield components. For each cultivar, above-ground and root biomass, root colonization (number and biomass of nodules) and the yield attributes (number of pods per plant, pod weight) were determined. Above-ground and root biomass, nodule weight and the yield attributes were determined by weighing sample parts after over-drying to constant weight at 65°C.

Data analyses

All data were tested for normality and homogeneity using the Shapiro-Wilk and Levene tests, respectively. Data for plant growth and yield parameters were statistically analyzed using univariate analysis with one-way analysis of variance (ANOVA) using the R software v3.4.4 (R Core Team, 2020). Significantly different means and standard deviation were separated using the Tukey (HSD) test at the 5% probability threshold.

RESULTS

Plant nodulation

The results showed that there was a significant difference ($p < 0.05$) in nodule number and nodule biomass between the inoculated and uninoculated treatments for all cultivars (Table 2). Irrespective of the peanut cultivar, plants in the *Bradyrhizobium* strain ISRA519 treatment were more nodulated than the other inoculated strains and the uninoculated plants, indicating that this strain had a high nodule occupancy capacity. However, the nodulation was more pronounced in some cultivars rather than in others. In particular, in the traditional short-cycle peanut cultivars *55-437* and *Fleur 11* and in the modern short-cycle cultivar *Sunu Gaal*, the ISRA519 strain had the highest nodule number and nodule dry weight compared to the modern long-cycle cultivars *Amoul Morom* and *Essamay*.

In the *Amoul Morom* cultivar, inoculation with the indigenous strains ISRA 453, ISRA519, ISRA534 and ISRA538, isolated from the *Fleur 11* cultivar significantly increased the number of nodules. Inoculation with ORS3644, isolated from *M. atropurpureum*, also increased nodule number with strain LMG9283, also

Table 2. Nodulation (number and biomass of nodules) of five peanut cultivars (*A. hypogaea*) under single inoculation with *Bradyrhizobium* sp. 65 days after planting.

Treatments	Peanut cultivars									
	<i>Amoul Morom</i>		<i>Essamaye</i>		<i>55-437</i>		<i>Fleur11</i>		<i>Sunu Gaal</i>	
	NNum	NDW (g)	NNum	NDW (g)	NNum	NDW (g)	NNum	NDW (g)	NNum	NDW (g)
<i>ISRA400</i>	43.0±6.22 ^f	0.04±0.01 ^{ab}	63.0±10.7 ^{cd}	0.06±0.01 ^{abc}	50.8±16.8 ^c	0.04±0.01 ^b	74.0±5.77 ^c	0.04±0.01 ^b	111±8.37 ^b	0.07±0.01 ^b
<i>ISRA453</i>	87.5±12.7 ^{bc}	0.05±0.01 ^{ab}	81.0±6.38 ^{bc}	0.05±0.01 ^{abc}	47.0±1.83 ^c	0.05±0.02 ^{ab}	110±16.1 ^{bc}	0.06±0.01 ^{ab}	68.5±3.70 ^b	0.06±0.02 ^b
<i>ISRA454</i>	60.0±16.1 ^{def}	0.05±0.01 ^{ab}	91.0±8.25 ^{ab}	0.04±0.01 ^{abc}	26.3±2.22 ^c	0.04±0.01 ^b	112±13.0 ^{bc}	0.06±0.01 ^{ab}	60.0±6.16 ^b	0.05±0.01 ^b
<i>ISRA519</i>	133.0±6.08 ^a	0.06±0.01 ^a	111 ±4.43 ^a	0.05±0.01 ^{abc}	469±80.8 ^a	0.09±0.06 ^a	306±64.2 ^a	0.07±0.01 ^a	477±94.0 ^a	0.20±0.03 ^a
<i>ISRA534</i>	114.0±6.81 ^{ab}	0.06±0.02 ^{ab}	92.0±4.76 ^{ab}	0.03±0.01 ^c	126±3.79 ^b	0.05±0.01 ^{ab}	136±10.0 ^b	0.05±0.01 ^{ab}	122±14.2 ^b	0.05±0.01 ^b
<i>ISRA538</i>	90.0±12.3 ^{bc}	0.06±0.01 ^{ab}	68.5±14.1 ^{bcd}	0.04±0.01 ^{abc}	66.3±10.4 ^{bc}	0.05±0.01 ^{ab}	75.0±3.5 ^c	0.05±0.01 ^{ab}	81.3±15.9 ^b	0.05±0.01 ^b
<i>ORS3640</i>	53.8±14.7 ^{ef}	0.05±0.01 ^{ab}	82.5±15.0 ^{bc}	0.05±0.02 ^{abc}	55.5±5.20 ^c	0.06±0.01 ^{ab}	121±27.4 ^{bc}	0.04±0.00 ^b	108±4.97 ^b	0.05±0.01 ^b
<i>ORS3644</i>	72.3±7.76 ^{cde}	0.04±0.01 ^{ab}	90.0±10.6 ^{abc}	0.06±0.01 ^{abc}	64.5±21.8 ^{bc}	0.03±0.01 ^b	111±13.2 ^{bc}	0.04±0.01 ^b	109±15.9 ^b	0.04±0.01 ^b
<i>LMG9283</i>	81.5±12.8 ^{cd}	0.04±0.01 ^{ab}	75.3±21.2 ^{bcd}	0.05±0.02 ^{abc}	64.5±4.51 ^{bc}	0.03±0.01 ^b	88.8±6.50 ^{bc}	0.04±0.01 ^b	89.5±15.2 ^b	0.06±0.02 ^b
<i>USD3187</i>	65.3±7.09 ^{cdef}	0.05±0.00 ^{ab}	64.8±4.57 ^{bcd}	0.06±0.01 ^{ab}	59.8±20.3 ^c	0.04±0.01 ^b	84.0±11.6 ^{bc}	0.05±0.01 ^{ab}	49.0±9.06 ^b	0.05±0.01 ^b
Control	45.3±3.77 ^f	0.04±0.01 ^b	48.0±12.4 ^d	0.06±0.01 ^a	48.75±2.06 ^c	0.02±0.01 ^b	73.5±7.94 ^c	0.05±0.01 ^{ab}	69.8±8.77 ^b	0.06±0.01 ^b
Mea±sd	76.3±12.8	0.05±0.01	78.9±19.6	0.05±0.01	94.5±25.0	0.04±0.03	117±6.7	0.05±0.01	123±16.9	0.07±0.04
CV (%)	13.921	21.098	14.413	22.319	28.319	16.608	19.899	18.749	24.821	20.529
pValue	1.39 e ^{-12***}	0.013*	3.47e ^{-07***}	0.004**	<2 e ^{-16***}	0.004**	4.16 e ^{-14***}	0.002**	<2 e ^{-16***}	4.72 e ^{-15***}

NNum (Nodule number); NDW (nodule dry weight); Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 *, 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). Values (mean ± standard deviation) with the same superscript letter within a column are not statistically different at the 5% probability according to Tukey test.

isolated from peanut. In contrast, the commercial strain USDA3187 showed no significant difference compared to the control. However, the nodule dry mass was significantly different only in plants inoculated with ISRA519 (Table 2).

In the *Essamaye* cultivar, plants inoculated with the indigenous strains ISRA453, ISRA454, ISRA519 and ISRA534 showed a significant increase in nodule formation compared to the control. In addition, ORS3640, isolated from siratro plants, also showed a significant increase in the number of nodules. The reference strains LMG9283 and USDA3187 showed no significant difference in nodule formation compared to the control. Thus, the native strains appear to be more efficient in increasing the number of nodules

in the *Essamaye* cultivar, and no significant difference in nodule dry mass was found between treatments (Table 2).

Compared to the control plants, only inoculation with ISRA519 and ISRA534 showed a significant increase in nodule numbers when inoculated on the traditional cultivars *55-437* and *Fleur 11*, and no significant difference was found between treatments for the nodule dry mass. For the cultivar *Sunu Gaal*, inoculation with ISRA519 showed a significant increase in nodule formation (Table 2).

Estimated leaf chlorophyll content

For the six cultivars, leaf chlorophyll content at 30, 45 and 65 DAP ranged from 25.6 to 40.1 (Table

S1), 30.5 to 44.2 (Table S2) and 25.5 to 39.3 (Table 3), respectively, and was higher for peanut cultivar *Amoul Morom*. The data showed no significant difference between the inoculated and non-inoculated plants, for most of the inoculated strains, irrespective of the cultivar. However, for cultivar *55-437*, the leaf chlorophyll content increased significantly at 30 DAP for plants inoculated with ISRA454, ORS3640 and LMG9283 (Table S1). At 45 DAP only the plants inoculated with ISRA534 and ISRA538 showed a significant increase in leaf chlorophyll content compared to the control (Table S2). At 65 DAP, inoculation with ISRA453 and ISRA454 showed a significant increase in leaf chlorophyll content compared to the control (Table 3). In addition, the leaf

Table 3. Estimated leaf chlorophyll content at 65 days after planting in response to peanut cultivars (*A. hypogaea*) single inoculation with *Bradyrhizobium* spp. Strains.

Treatments	Peanut cultivars				
	<i>Amoul Morom</i>	<i>Essamaye</i>	<i>55-437</i>	<i>Fleur11</i>	<i>Sunu Gaal</i>
<i>ISRA400</i>	37.5±0.96 ^{ab}	29.3±1.85 ^{bc}	28.0±1.24 ^{ab}	28.5±3.80 ^b	32.1±2.16 ^{ab}
<i>ISRA453</i>	39.3±1.56 ^a	33.6±1.08 ^a	30.2±1.79 ^a	32.0±1.26 ^{ab}	35.5±2.39 ^a
<i>ISRA454</i>	39.3±1.93 ^a	31.9±0.88 ^{ab}	30.1±1.96 ^a	33.5±1.71 ^a	33.6±3.20 ^{ab}
<i>ISRA519</i>	37.6±0.81 ^{ab}	30.1±2.00 ^{abc}	27.2±3.41 ^{ab}	30.5±0.59 ^{ab}	34.3±3.28 ^{ab}
<i>ISRA534</i>	37.5±1.99 ^{ab}	30.8±1.34 ^{abc}	29.1±1.42 ^{ab}	29.6±1.42 ^{ab}	34.4±1.47 ^{ab}
<i>ISRA538</i>	35.0±2.26 ^b	31.3±1.63 ^{abc}	28.0±1.72 ^{ab}	29.4±1.82 ^{ab}	32.1±2.32 ^{ab}
<i>ORS3640</i>	38.1±0.67 ^{ab}	28.5±1.30 ^{bc}	27.6±1.72 ^{ab}	29.1±1.51 ^{ab}	32.2±2.24 ^{ab}
<i>ORS3644</i>	35.2±1.85 ^{ab}	29.8±1.77 ^{abc}	28.8±1.73 ^{ab}	29.6±1.38 ^{ab}	32.4±2.27 ^{ab}
<i>LMG9283</i>	37.9±1.62 ^{ab}	30.7±1.86 ^{abc}	26.6±1.67 ^{ab}	28.3±1.02 ^b	33.4±1.37 ^{ab}
<i>USD3187</i>	35.7±2.95 ^{ab}	30.7±2.34 ^{abc}	28.0±0.30 ^{ab}	30.7±2.76 ^{ab}	32.8±1.09 ^{ab}
Control	34.5±1.64 ^b	27.9±1.26 ^c	25.5±1.01 ^b	28.2±1.75 ^b	29.6±1.49 ^{ab}
Mea±sd	37.1±2.25	30.4±2.09	28.1±2.08	29.9±2.31	33.0±2.47
CV (%)	4.632	5.356	6.355	6.409	6.736
pValue	0.002 ^{**}	0.0019 ^{**}	0.021 [*]	0.009 ^{**}	0.069 ^{ns}

Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 ', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). Values (mean ± standard deviation) with the same superscript letter within a column are not statistically different at the 5% probability according to Tukey test.

chlorophyll content of the leaves for the control plants was lower than that of the inoculated plants for all cultivars.

Growth response of peanut cultivars to bradyrhizobial inoculation

The results showed that the traditional cultivars responded better to the bradyrhizobial inoculation than the modern cultivars, with the exception of *Sunu Gaal*, which is genetically close to *Fleur 11* (Faye I. personal communication). Of the ten treatments tested in this study, 40% showed the ability to increase plant height in the cultivar *Amoul Morom*, 20% in *Essamaye*, 80% in *55-437*, 20% in *Fleur 11*, and 50% in *Sunu Gaal*. Inoculation with 30 and 20% of our collection showed the ability to improve biomass production in the traditional cultivars *55-437* and *Fleur 11*, respectively. However, none of the bradyrhizobial strains improved this growth parameter in the modern cultivars *Amoul Morom*, *Essamaye* and *Sunu Gaal*.

For cultivar *55-437*, only the reference strain LMG9283 and the indigenous strain *ISRA400* showed no significant difference compared to the control (Table 4). In contrast to the LMG9283, the *ISRA400* significantly increased the plant height but only at 30 DAP (Table S3). The other inoculated strains showed a significant increase in plant height at 65 DAP. The highest plant height (43.2cm ± 4.74cm) was obtained with strain *ORS3644*, isolated from siratro. Four indigenous strains (*ISRA400*, *ISRA453*, *ISRA454* and *ISRA534*) showed a significant increase in

plant height for the *Amoul Morom* cultivar at both 45 and 65 DAP (Table 4 and Table S4). Only the indigenous strain *ISRA453* showed a significant increase for the cultivar *Essamaye* at 65 DAP. Interestingly, this strain also showed a significant increase in plant height for the cultivars *Fleur 11* (at 65 DAP) and *Sunu Gaal* (at 45 and 65 DAP). Only the indigenous strains *ISRA453*, *ISRA519*, *ISRA534* and *ISRA538* isolated from cultivar *Fleur 11* showed a significant increase in plant height with cultivar *Sunu Gaal*. However, none of the inoculated strains showed a significant difference in collar diameter for all cultivars (Table 4). Based on these results, it can be assumed that the peanut cultivar *55-437* responded better to the bradyrhizobial inoculation in terms of growth.

Peanut dry matter and yield attributes

Both shoot and root dry biomass showed no significant difference between treatments for the modern peanut cultivars *Amoul Morom*, *Essamaye* and *Sunu Gaal*, but were significantly higher for the traditional cultivars *55-437* and *Fleur 11* when inoculated with *ORS3644* and LMG9283 for the former and *ISRA453* and *ISRA454* for the latter (Table 5).

Yield characteristics were improved in 20% of the treatments for the cultivar *Essamaye* and in 10% of the treatments for the cultivars *55-437*, *Fleur 11* and *Amoul Morom*. As the plants were harvested before maturity, it is expected that the yield at pod maturity of the inoculated plants will be significantly higher. In terms of pod yield attributes, the inoculated strains *ISRA453*, *ISRA454*,

Table 4. Growth (plant height and collar diameter) response of peanut cultivars (*A. hypogaea*) to single inoculation with *Bradyrhizobium* spp. 65 days after planting.

Treatments	Peanut cultivars									
	<i>Amoul Morom</i>		<i>Essamaye</i>		<i>55-437</i>		<i>Fleur11</i>		<i>Sunu Gaal</i>	
	Height (cm)	CD (mm)	Height (cm)	CD (mm)	Height (cm)	CD (mm)	Height (cm)	CD (mm)	Height (cm)	CD (mm)
<i>ISRA400</i>	29.3±2.56 ^a	7.70±0.67 ^a	30.2±1.11 ^c	6.17±0.56 ^{ab}	33.8±2.11 ^{de}	5.65±0.27 ^{ab}	30.3±2.12 ^d	5.62±0.36 ^{ab}	31.4±1.68 ^d	5.03±0.53 ^a
<i>ISRA453</i>	28.1±1.48 ^{ab}	6.20±0.76 ^b	35.2±1.17 ^a	4.93±0.41 ^{bc}	40.8±4.75 ^{abc}	5.73±0.48 ^{ab}	36.5±1.96 ^a	5.03±0.37 ^{ab}	36.7±3.49 ^{abc}	5.02±0.55 ^a
<i>ISRA454</i>	27.8±0.91 ^{ab}	7.30±0.38 ^{ab}	30.6±0.48 ^{bc}	5.91±0.58 ^{ab}	37.7±0.79 ^{abcd}	5.70±0.54 ^{ab}	36.1±0.70 ^{ab}	5.08±0.43 ^{ab}	32.9±1.55 ^{cd}	5.99±0.39 ^a
<i>ISRA519</i>	27.2±0.84 ^{abc}	7.16±0.08 ^{ab}	26.5±0.71 ^d	5.27±0.17 ^{abc}	36.4±4.15 ^{bcd}	5.39±0.17 ^{ab}	30.5±2.40 ^d	4.84±0.56 ^{ab}	38.5±1.74 ^{ab}	4.96±0.56 ^a
<i>ISRA534</i>	28.1±1.01 ^{ab}	6.77±0.42 ^{ab}	33.0±3.29 ^{ab}	5.23±0.18 ^{abc}	42.9±1.55 ^{ab}	5.09±0.44 ^{ab}	34.1±0.77 ^{abcd}	4.74±0.40 ^b	36.9±2.46 ^{abc}	5.22±0.18 ^a
<i>ISRA538</i>	26.3±1.26 ^{bc}	7.07±0.05 ^{ab}	30.7±6.09 ^c	4.60±1.04 ^c	40.1±2.39 ^{abcd}	4.76±0.32 ^b	32.6±0.97 ^{abcd}	5.12±0.38 ^{ab}	40.6±0.49 ^a	4.94±0.37 ^a
<i>ORS3640</i>	26.1±0.48 ^{bc}	6.64±0.41 ^{ab}	29.9±1.66 ^c	6.47±0.52 ^a	38.6±1.38 ^{abcd}	5.42±0.44 ^{ab}	35.2±1.14 ^{abc}	6.02±1.13 ^a	34.2±0.68 ^{bcd}	5.27±0.47 ^a
<i>ORS3644</i>	27.4±0.87 ^{abc}	7.77±0.83 ^a	35.8±1.97 ^a	5.35±0.21 ^{abc}	43.2±4.74 ^a	5.32±0.30 ^{ab}	35.5±1.08 ^{abc}	5.14±0.31 ^{ab}	36.6±0.63 ^{abc}	4.89±0.64 ^a
<i>LMG9283</i>	25.9±1.80 ^{bc}	7.09±0.69 ^{ab}	31.9±0.84 ^{bc}	5.81±0.65 ^{abc}	35.7±0.81 ^{cd}	5.94±0.31 ^a	32.0±2.04 ^{bcd}	5.33±0.54 ^{ab}	31.6±1.49 ^d	5.45±0.24 ^a
<i>USD3187</i>	25.2±1.44 ^{bc}	7.84±0.65 ^a	30.7±0.46 ^{bc}	5.71±.26 ^{abc}	33.5±1.29 ^{de}	5.28±0.22 ^{ab}	34.1±2.81 ^{abcd}	4.88±0.46 ^{ab}	31.1±2.53 ^d	5.23±0.64 ^a
Control	24.5±0.44 ^c	6.75±0.67 ^{ab}	31.5±1.35 ^{bc}	6.28 ±0.41 ^a	27.7±1.33 ^e	5.37±0.84 ^{ab}	31.6±2.06 ^{cd}	5.52±0.28 ^{ab}	30.9±1.63 ^d	5.08±0.86 ^a
Mea±sd	26.9±1.80	7.11±0.70	31.5±3.21	5.61±0.73	37.3±5.03	5.42±0.49	33.5±2.64	5.21±0.59	34.5±3.56	5.19±0.56
CV (%)	4.954	8.002	7.439	9.205	7.294	7.958	5.316	10.058	5.522	10.233
pValue	0.0007***	0.008**	0.0003***	0.0002***	4.11 e ^{-08***}	0.035*	3.05 e ^{-05***}	0.050*	5.13 e ^{-08***}	0.231 ^{ns}

CD (Collar Diameter); Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 ', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). Values (mean ± standard deviation) with the same superscript letter within a column are not statistically different at the 5% probability according to Tukey test.

ISRA519, *ISRA538* and *LMG9283* showed a better agronomic performance for the cultivars *55-437*, *Fleur 11*, *Essamaye* and *Amoul Morom*, respectively. Some of the other strains showed higher pod number and pod dry mass than the control, but these were not statistically significant (Table 6). Cultivar *Fleur 11* had yielded more than the other four cultivars with a maximum of $1.90 \pm 0.78 \text{ g plant}^{-1}$ in the *ISRA519* treatment.

DISCUSSION

Biofertilizers play an important role in increasing peanut (*A. hypogaea* L.) yield by scavenging atmospheric nitrogen (Chotangui et al., 2022), increasing phosphorus availability (Xiang et al.,

2022) or by promoting growth (Frezarin et al., 2023). The aim of this study was to isolate the most specific and effective *Bradyrhizobium* spp. strain for five peanut cultivars and to determine the degree of variability in the cultivar response toward inoculation. It was observed that the strains tested in the present study promoted an increase in various parameters analyzed. Specifically, indigenous *Bradyrhizobium* isolates were more effective in improving the growth, leaf chlorophyll content and yield parameters compared to the reference strains, and the effectiveness of the inoculated strains depended on the peanut genotype used.

Peanut is endowed with nitrogen-fixing ability and can form nodules if it finds compatible soil rhizobia. In general, nodule formation depends on

the number of infective rhizobia available at the root infection sites. The more infective rhizobia there is, the greater the number of nodules, although nodulation is also governed by both bacteria and intrinsic plant factors. In this study, five peanut cultivars were individually inoculated with 5 mL of a rhizobial suspension containing 10^8 cells mL^{-1} . Although the soil substrate used contains a rhizobial population greater than 10^3 cells g^{-1} (Sene et al., 2010), it was expected that the peanut cultivars would respond positively to rhizobial inoculation in terms of nodulation. The results showed that there was a significant difference in nodule number and nodule biomass between the inoculated and uninoculated treatments for all cultivars. However, irrespective of the peanut cultivar, plants in the

Table 5. Biomass production (above-ground and root biomass) of peanut cultivars at harvest.

Treatments	Peanut cultivars									
	<i>Amoul Morom</i>		<i>Essamaye</i>		<i>55-437</i>		<i>Fleur11</i>		<i>Sunu Gaal</i>	
	SDW (g)	RDW (g)	SDW (g)	RDW (g)	SDW (g)	RDW (g)	SDW (g)	RDW (g)	SDW (g)	RDW (g)
<i>ISRA400</i>	4.02±0.36 ^a	1.07±0.01 ^a	3.15±0.68 ^a	1.14±0.07 ^{ab}	2.55±0.58 ^{ab}	0.72±0.21 ^{ab}	3.19±0.39 ^{abc}	0.77±0.10 ^a	3.45±0.26 ^a	0.67±0.19 ^a
<i>ISRA453</i>	3.98±0.14 ^a	1.06±0.02 ^a	3.23±1.04 ^a	0.63±0.06 ^c	2.63±0.51 ^{ab}	0.86±0.14 ^{ab}	3.70±0.43 ^{ab}	0.77±0.07 ^a	3.91±0.39 ^a	0.72±0.25 ^a
<i>ISRA454</i>	4.06±0.43 ^a	1.11±0.04 ^a	4.02±0.35 ^a	0.92±0.19 ^{abc}	3.01±0.51 ^{ab}	0.94±0.11 ^{ab}	3.94±0.31 ^a	0.71±0.11 ^a	2.44±0.23 ^a	0.60±0.16 ^a
<i>ISRA519</i>	4.53±0.64 ^a	1.25±0.22 ^a	2.66±0.39 ^a	0.75±0.19 ^{bc}	2.50±0.37 ^{ab}	0.72±0.06 ^{ab}	2.82±0.06 ^{bc}	0.65±0.19 ^a	3.18±0.39 ^a	0.52±0.08 ^a
<i>ISRA534</i>	3.71±0.72 ^a	1.18±0.33 ^a	3.53±1.08 ^a	0.80±0.10 ^{bc}	3.00±0.30 ^{ab}	0.80±0.14 ^{ab}	3.64±0.21 ^{abc}	0.74±0.10 ^a	3.36±0.76 ^a	0.54±0.05 ^a
<i>ISRA538</i>	3.98±0.58 ^a	1.00±0.08 ^a	2.65±0.24 ^a	0.73±0.14 ^c	2.52±0.78 ^{ab}	0.63±0.12 ^{ab}	2.86±0.40 ^{abc}	0.69±0.09 ^a	3.89±0.89 ^a	0.63±0.07 ^a
<i>ORS3640</i>	3.97±0.88 ^a	1.18±0.10 ^a	3.18±0.65 ^a	0.91±0.27 ^{abc}	2.96±0.60 ^{ab}	0.97±0.21 ^a	3.63±0.67 ^{abc}	0.69±0.20 ^a	3.74±0.87 ^a	0.62±0.17 ^a
<i>ORS3644</i>	3.92±0.17 ^a	1.22±0.28 ^a	3.03±0.56 ^a	0.85±0.12 ^{abc}	3.27±0.86 ^a	0.78±0.19 ^{ab}	3.62±0.29 ^{abc}	0.85±0.13 ^a	3.41±0.90 ^a	0.64±0.01 ^a
<i>LMG9283</i>	3.53±0.39 ^a	1.02±0.03 ^a	3.08±0.71 ^a	0.91±0.09 ^{abc}	3.85±0.19 ^a	0.78±0.16 ^{ab}	2.83±0.46 ^{abc}	0.89±0.07 ^a	3.15±1.05 ^a	0.56±0.08 ^a
<i>USD3187</i>	3.97±0.20 ^a	1.10±0.08 ^a	3.85±0.19 ^a	1.22±0.19 ^a	2.69±1.23 ^{ab}	0.91±0.14 ^{ab}	3.38±0.86 ^{abc}	0.60±0.02 ^a	2.44±0.30 ^a	0.80±0.10 ^a
Control	3.36±0.70 ^a	0.90 ± 0.11 ^a	2.73±0.25 ^a	0.94±0.22 ^{abc}	1.45±0.47 ^b	0.60±0.10 ^b	2.56±0.55 ^c	0.75±0.11 ^a	2.91±1.24 ^a	0.72±0.07 ^a
Mea±sd	0.91±0.55	1.10±0.17	3.19±0.71	0.89±0.22	2.77±0.80	0.79±0.17	3.29±0.60	0.74±0.13	3.24±0.81	0.64±0.14
CV (%)	13.525	13.833	19.806	18.168	23.242	18.934	13.927	16.315	22.841	20.534
pValue	0.266 ^{ns}	0.091 ^{ns}	0.057 ^{ns}	0.0005 ^{***}	0.004 ^{**}	0.020 [*]	0.001 ^{**}	0.083 ^{ns}	0.097 ^{ns}	0.13 ^{ns}

SDW (Shoot dry weight); RDW (Root dry weight); Significant codes: 0 '****', 0.001 '***', 0.01 '**', 0.05 '*', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). Values (mean ± standard deviation) with the same superscript letter within a column are not statistically different at the 5% probability according to Tukey test.

Bradyrhizobium strain ISRA519 treatment were more nodulated than the other inoculated strains and the uninoculated plants, indicating that this strain had a high capacity for nodule initiation and subsequent nodule development. The result also showed that this strain was the only inoculant to have a significant effect on pooled nodule dry weight. This result is consistent with a previous report by Zaiya et al. (2018), who classified ISRA519 as the most nodulating isolate.

The data of this study support a cultivar-*Bradyrhizobium* specificity. The results showed that nodulation was more pronounced in some cultivars than in others. In particular, strain ISRA519 showed the highest nodule number and nodule dry weight with the traditional peanut

cultivars *55-437* and *Fleur 11* and the modern cultivar *Sunu Gaal* (which is genetically very close to the cultivar *Fleur 11*) compared to the modern cultivars *Amoul Morom* and *Essamay*. In contrast, most of the other inoculated *Bradyrhizobium* strains showed increased nodulation with the latter cultivars rather than with the former. This confirmed the role of plant genotype in nodule formation with inoculated rhizobial strains already reported in soybean (*Glycine max*) (Meghvansi et al., 2008). This may have been the reason for the different compatibility of the tested isolates with the tested peanut cultivars. This observation was consistent with the findings of Chen et al. (2003) in Argentine soil and Argaw (2017) in Ethiopian soil that there was a cultivar-*Bradyrhizobium*

strain specificity. On the other hand, the indigenous strains seemed to be more efficient in increasing the number of nodules compared to the reference strains, regardless of the cultivar used. This is particularly observed for the exotic strain USDA3187 and is probably due to the fact that the native strains are better adapted and therefore have an advantage in nodule colonization. Similarly, previous results where rhizobial inoculation had no significant effect on nodulation have been reported (Castro et al., 1999; Bogino et al., 2006, 2008; Chotangui et al., 2022) and support our data.

Peanut was considered a highly "promiscuous" species (Bogino et al., 2006), being nodulated by a wide variety of rhizobia. Thus, the response of

Table 6. Yield attributes (number of pods per plant, pod weight) of peanut cultivars at harvest.

Treatments	Peanut cultivars									
	<i>Amoul Morom</i>		<i>Essamaye</i>		<i>55-437</i>		<i>Fleur11</i>		<i>Sunu Gaal</i>	
	Pod number	Weight of pods (g)	Pod number	Weight of pods (g)	Pod number	Weight of pods (g)	Pod number	Weight of pods (g)	Pod number	Weight of pods (g)
<i>ISRA400</i>	7.25±0.96 ^a	0.59±0.11 ^{ab}	5.25±1.71 ^a	0.45±0.23 ^c	3.25±1.26 ^{ab}	0.76±0.49 ^{ab}	5.25±1.50 ^a	1.06±0.28 ^b	5.00±1.41 ^{ab}	0.85±0.20 ^{ab}
<i>ISRA453</i>	5.00±1.41 ^{ab}	0.48±0.18 ^{ab}	5.50±1.29 ^a	1.55±0.22 ^a	3.25±0.96 ^{ab}	0.88±0.21 ^{ab}	5.75±0.96 ^a	1.55±0.33 ^{ab}	7.00±1.41 ^a	0.66±0.20 ^{ab}
<i>ISRA454</i>	4.75±0.96 ^{ab}	0.52±0.10 ^{ab}	5.50±2.38 ^a	0.78±0.11 ^c	6.00±1.63 ^a	1.08±0.30 ^a	7.00±0.82 ^a	1.56±0.27 ^{ab}	4.25±0.96 ^{ab}	0.49±0.10 ^b
<i>ISRA519</i>	5.75±0.96 ^{ab}	0.81±0.25 ^{ab}	5.00±0.82 ^a	0.81±0.27 ^c	4.25±0.96 ^{ab}	0.42±0.15 ^b	7.00±1.83 ^a	1.90±0.78 ^a	6.50±1.29 ^{ab}	0.54±0.10 ^{ab}
<i>ISRA534</i>	4.00±1.00 ^{ab}	0.64±0.31 ^{ab}	5.75±0.96 ^a	0.74±0.07 ^c	4.75±0.96 ^{ab}	0.44±0.24 ^{ab}	7.50±1.00 ^a	1.61±0.20 ^{ab}	4.75±1.71 ^{ab}	0.61±0.06 ^{ab}
<i>ISRA538</i>	6.50±2.52 ^{ab}	0.90±0.22 ^a	3.50±0.58 ^a	0.50±0.14 ^c	3.50±0.58 ^{ab}	0.39 ± 0.18 ^b	6.50±1.29 ^a	1.30±0.20 ^{ab}	5.33±0.58 ^{ab}	0.59±0.09 ^{ab}
<i>ORS3640</i>	6.50±1.29 ^{ab}	0.66±0.17 ^{ab}	5.25±2.06 ^a	0.83±0.21 ^c	5.25±1.50 ^{ab}	0.87±0.39 ^{ab}	7.75±1.26 ^a	1.49±0.10 ^{ab}	6.25±1.26 ^{ab}	0.95±0.12 ^a
<i>ORS3644</i>	4.00±0.82 ^b	0.48±0.06 ^{ab}	5.50±0.58 ^a	0.89±0.15 ^{bc}	5.25±1.50 ^{ab}	0.89±0.19 ^{ab}	6.50±1.29 ^a	1.28±0.19 ^{ab}	6.00±2.45 ^{ab}	0.69±0.22 ^{ab}
<i>LMG9283</i>	5.00±0.82 ^{ab}	0.48±0.17 ^{ab}	4.25±0.50 ^a	1.35±0.30 ^{ab}	4.75±1.71 ^{ab}	0.87±0.23 ^{ab}	5.25±0.96 ^a	1.00±0.34 ^b	3.75±1.26 ^{ab}	0.78±0.36 ^{ab}
<i>USD3187</i>	6.33±0.58 ^{ab}	0.63±0.03 ^{ab}	4.50±0.58 ^a	0.90±0.22 ^{bc}	5.00±0.82 ^{ab}	0.82±0.22 ^{ab}	5.75±2.36 ^a	0.98±0.17 ^b	3.25±1.50 ^b	0.53±0.13 ^{ab}
Control	5.00±1.41 ^{ab}	0.41±0.26 ^b	5.50±0.58 ^a	0.72±0.23 ^c	2.75±0.96 ^b	1.03±0.04 ^{ab}	4.75±1.50 ^a	1.06±0.24 ^b	4.25±0.96 ^{ab}	0.59±0.10 ^{ab}
Mea±sd	5.48±1.52	0.60±0.21	5.05±1.29	0.86±0.36	4.36±1.46	0.77±0.33	6.27±1.56	1.34±0.41	5.12±1.72	0.66±0.21
CV (%)	23.403	29.791	25.118	24.012	27.925	34.656	22.460	24.608	28.105	26.672
pValue	0.018*	0.014*	0.34 ^{ns}	2.46 e ^{-07***}	0.010*	0.005**	0.069 ^{ns}	0.004**	0.013*	0.017*

Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 ', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). Values (mean ± standard deviation) with the same superscript letter within a column are not statistically different at the 5% probability according to Tukey test.

peanut to rhizobial inoculation has always been questionable worldwide: India (Gaur et al., 1974; Nambiar, 1985; Wange, 1989; Joshi et al., 2008), Israel (Schiffmann and Alper, 1968), Brazil (Cardoso et al., 2009), Argentina (Castro et al., 1999; Bogino et al., 2006; 2008), and Cameroon (Chotangui et al., 2022). A positive response has already been observed by Sene et al. (2010) in the selected site, that is, Sangalkam, where the population size of the indigenous rhizobia is greater than 10³ cells g⁻¹. Indeed, most of the inoculated plants of cultivars 55-437 were positively affected at 45 DAP and positive responses were also observed at 65 DAP in terms of plant height, shoot dry weight and pod number and dry matter. Consistent with its effect on

nodulation, the indigenous strain ISRA519 significantly affected plant growth of cultivars 55-437 and *Sunu Gaal* and pod yield parameters of cultivar *Fleur 11*, but no significant increase was observed for the remaining modern cultivars. This confirms the cultivar-*Bradyrhizobium* specificity found for nodulation and supported by several authors (Chen et al., 2003; Meghvansi et al., 2008; Argaw, 2017). Although the precise drivers of the variation in root nodulation rates and host plant response among different crop genotypes remain poorly understood, it has been suggested, for instance, that modern crop breeding may have negatively affected the ability to establish microbial symbioses (Martín-Robles et al., 2018, 2020; Sawers et al., 2018). As breeding programs

generally aim to maximize crop yield in high-input production systems, it is likely that a breeding process accompanied by high fertilization rates may select crop genotypes that are less responsive to the root microbial symbioses, as has been suggested by Parvin et al. (2021) with arbuscular mycorrhizal fungi and rice cultivars.

Although the inoculated plants performed better than the non-inoculated plants, the expected improvements were not achieved for some inoculated strains as most of the isolates were previously selected for their efficacy on peanut and other legume species (Sene et al., 2010, 2012, 2013; Zaiya et al., 2018). The results showed that most of the inoculated strains that have induced improvements in plant growth and

yield parameters were from the indigenous collection of bradyrhizobia. Inoculation with ISRA453 and ISRA454 showed the better to increase plant growth and biomass production in all cultivars. The performance of the indigenous bradyrhizobia was demonstrated in the work of Zaiya et al. (2018) and confirmed in the present study. This is reflected in the leaf chlorophyll content shown in the SPAD readings, which indicates improved nitrogen fixation of these inoculated strains compared to the reference strain USDA3187 formulated for peanut cultivation. Indeed, chlorophyll pigment is an indicator of the level of nitrogen assimilation and is responsible for the green color of the leaves (Deroche, 1983). The efficiency of nitrogen fixation in peanut was previously reported to result in the accumulation of nitrogen in plants which in turn reflected the synthesis of chlorophyll (Nageswara et al., 2001). The failure of inoculation with the *Bradyrhizobium* strain USDA3187 to elicit a response in peanut cultivars could be attributed to the presence of highly competitive but ineffective indigenous strains that exclude the inoculated strains from occupying the nodules, as has been suggested in previous work by several authors (Castro et al., 1999; Bogino et al., 2006, 2008; Sene et al., 2010). In contrast, *Bradyrhizobium* spp. LMG9283 has promoted an increase in plant height and shoot dry weight of peanut cultivar 55-437 and improved yield parameters of cultivar *Essamay*. The strain LMG9283 was isolated in the Senegalese peanut basin and has already been recognized for its agronomic performance on peanut (Dhery and Dreyfus, 1991; Sene et al., 2010). Thus, the indigenous bradyrhizobia seem to be more efficient in increasing nodulation, plant growth and yield parameters.

Conclusion

The demand for microbial inoculants is increasing, driven by the need for sustainable and environmentally friendly agricultural practices and safer and healthier food. In order to select the best *Bradyrhizobium* spp. inoculants for Senegalese peanut cultivars, it was hypothesized that the response of peanut toward rhizobial inoculation is cultivar dependent and that there is a different degree of variability between traditional and modern cultivars. The results of this study showed that the strains tested promoted increases in various parameters analyzed. Specifically, indigenous *Bradyrhizobium* isolates were more effective in improving the growth, leaf chlorophyll content and yield parameters compared to the reference strains. This suggests that inoculation of peanut cultivars with exotic inoculants to improve plant growth and yield parameters is not necessary in the study soil. According to this study, it would be useful to promote the use of indigenous strains that perform well with the peanut cultivars studied. We also showed that the efficacy of the inoculated strains depended on the peanut genotype used and the result highlighted the need for cultivar-

specific selection of *Bradyrhizobium* to reap the benefits of nitrogen fixation and improve inoculation success in peanut. In addition, traditional peanut cultivars such as 55-437 responded better than the modern cultivars, demonstrating the differential feedback between peanut cultivars and *Bradyrhizobium* spp. partners. As the response of peanut to rhizobial inoculation has been questionable in West Africa, the increase in yield of the tested peanut cultivars should be considered as new promising data for the adoption of rhizobium technology for peanut improvement. Yet, this cannot be considered as a success of inoculation of peanut with rhizobial strains and field inoculation over several years is required.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

This study was funded by the Université Cheikh Anta Diop (UCAD) Internal Research Support Fund and the consortium Research Center for International Development (CRDI)/Ministry of Higher Education, Research and Innovation (MESRI) from Senegal (Program SGC12). The authors thank Omar Salif Guèye (for technical assistance and support) and Dr Samba Laha Ka (for help with data analysis).

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SUPPLEMENTARY DATA

Table S1. Leaf chlorophyll content at 30 days after planting in response to peanut cultivars inoculation with *Bradyrhizobium* sp. Strains.

Treatments	Peanut cultivars				
	<i>Amoul morom</i>	<i>Essamaay</i>	<i>55-437</i>	<i>Fleur 11</i>	<i>Sunu Gaal</i>
<i>ISRA400</i>	38.1 ± 1.06 ^a	33.0 ± 2.39 ^a	31.0 ± 3.37 ^a	33.3 ± 1.69 ^{abc}	30.2 ± 2.98 ^a
<i>ISRA453</i>	39.0 ± 3.16 ^a	31.0 ± 1.04 ^a	28.0 ± 0.95 ^{ab}	30.3 ± 1.02 ^{bc}	30.2 ± 3.29 ^a
<i>ISRA454</i>	39.0 ± 0.91 ^a	35.0 ± 4.42 ^a	31.9 ± 1.40 ^a	33.7 ± 2.47 ^{ab}	32.7 ± 0.78 ^a
<i>ISRA519</i>	37.1 ± 3.72 ^a	29.8 ± 1.51 ^a	27.9 ± 1.30 ^{ab}	31.4 ± 1.19 ^{abc}	30.8 ± 1.84 ^a
<i>ISRA534</i>	36.3 ± 0.70 ^a	31.0 ± 2.21 ^a	30.5 ± 1.60 ^{ab}	29.1 ± 0.61 ^c	32.8 ± 4.16 ^a
<i>ISRA538</i>	39.2 ± 0.70 ^a	31.3 ± 1.20 ^a	28.6 ± 2.40 ^{ab}	31.8 ± 1.23 ^{abc}	32.1 ± 2.72 ^a
<i>ORS3640</i>	37.0 ± 1.26 ^a	30.6 ± 1.05 ^a	31.0 ± 1.16 ^a	35.6 ± 3.61 ^a	33.2 ± 2.09 ^a
<i>ORS3644</i>	40.1 ± 2.73 ^a	32.8 ± 1.13 ^a	30.2 ± 1.54 ^{ab}	29.4 ± 1.36 ^{bc}	33.2 ± 0.48 ^a
<i>LMG9283</i>	37.6 ± 2.87 ^a	34.1 ± 2.59 ^a	31.3 ± 0.41 ^a	31.7 ± 2.21 ^{abc}	32.0 ± 3.52 ^a
<i>USD3187</i>	38.2 ± 1.83 ^a	34.5 ± 4.94 ^a	29.6 ± 1.20 ^{ab}	31.1 ± 1.68 ^{bc}	33.1 ± 2.66 ^a
Control	35.9 ± 1.47 ^a	29.9 ± 2.31 ^a	25.6 ± 4.15 ^b	28.9 ± 0.81 ^c	29.7 ± 1.80 ^a
Mea ± sd	38.0 ± 2.26	32.1 ± 2.90	29.6 ± 2.56	31.5 ± 2.56	31.8 ± 2.63
CV (%)	5.689	8.068	6.971	5.795	8.234
pValue	0.23 ^{ns}	0.0549 ^{ns}	0.000144 ^{***}	3.05 e ⁻⁰⁵ ^{***}	0.437 ^{ns}

Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 ', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). In columns, means with identical superscript letters are statistically equivalent at the 5% probability level.

Table S2. Leaf chlorophyll content at 45 days after planting in response to peanut cultivars inoculation with *Bradyrhizobium* sp. Strains.

Treatments	Peanut cultivars				
	<i>Amoul morom</i>	<i>Essamaay</i>	<i>55-437</i>	<i>Fleur 11</i>	<i>Sunu Gaal</i>
<i>ISRA400</i>	39.1 ± 1.54 ^{abc}	34.5 ± 1.56 ^a	32.4 ± 2.03 ^{ab}	32.6 ± 0.41 ^a	34.2 ± 2.44 ^a
<i>ISRA453</i>	42.0 ± 1.68 ^{ab}	35.9 ± 2.58 ^a	32.1 ± 1.72 ^{ab}	35.4 ± 2.34 ^a	38.5 ± 1.76 ^a
<i>ISRA454</i>	39.3 ± 2.79 ^{abc}	34.0 ± 1.91 ^a	32.0 ± 0.57 ^{ab}	33.6 ± 1.73 ^a	34.3 ± 2.85 ^a
<i>ISRA519</i>	41.7 ± 1.84 ^{abc}	35.1 ± 0.54 ^a	33.4 ± 3.68 ^{ab}	35.3 ± 2.50 ^a	35.9 ± 4.09 ^a
<i>ISRA534</i>	41.4 ± 0.85 ^{abc}	37.2 ± 3.12 ^a	36.8 ± 2.21 ^a	33.0 ± 1.25 ^a	38.7 ± 1.08 ^a
<i>ISRA538</i>	44.2 ± 4.65 ^a	36.3 ± 3.81 ^a	35.7 ± 2.33 ^a	36.2 ± 2.62 ^a	35.5 ± 3.32 ^a
<i>ORS3640</i>	38.5 ± 0.52 ^{bc}	35.2 ± 2.51 ^a	32.4 ± 1.40 ^{ab}	33.1 ± 1.45 ^a	34.3 ± 1.44 ^a
<i>ORS3644</i>	40.1 ± 1.84 ^{abc}	34.1 ± 1.30 ^a	33.2 ± 2.28 ^{ab}	32.4 ± 3.39 ^a	34.3 ± 2.62 ^a
<i>LMG9283</i>	36.6 ± 1.47 ^c	35.5 ± 1.79 ^a	31.9 ± 2.39 ^{ab}	34.3 ± 1.07 ^a	33.3 ± 4.02 ^a
<i>USD3187</i>	38.4 ± 2.27 ^{bc}	35.0 ± 1.89 ^a	32.3 ± 0.51 ^{ab}	34.3 ± 2.59 ^a	35.1 ± 1.46 ^a
Control	38.3 ± 0.59 ^{bc}	33.9 ± 1.93 ^a	30.5 ± 1.24 ^b	32.4 ± 1.45 ^a	33.0 ± 1.14 ^a
Mea ± sd	40.0 ± 2.83	35.1 ± 2.21	33.0 ± 2.49	33.9 ± 2.22	35.2 ± 2.90
CV (%)	5.398	6.408	6.202	6.097	7.332
P value	0.00148 ^{**}	0.591 ^{ns}	0.0073 ^{**}	0.134 ^{ns}	0.0517 ^{ns}

Significant codes: 0 ****, 0.001 ***, 0.01 **, 0.05 ', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd (mean ± standard deviation); CV (coefficient of variation). In columns, means with identical superscript letters are statistically equivalent at the 5% probability level.

Table S3. Plant height (cm) of peanut cultivars at 30 days after planting under inoculation with *Bradyrhizobium* sp. Strains.

Treatments	Peanut cultivars				
	<i>Amoul Morom</i>	<i>Essamaay</i>	<i>55-437</i>	<i>Fleur 11</i>	<i>Sunu Gaal</i>
<i>ISRA400</i>	19.2 ± 0.85 ^a	20.0 ± 2.13 ^b	28.2 ± 1.55 ^{abcd}	22.3 ± 1.29 ^{ab}	24.1 ± 2.66 ^{abc}
<i>ISRA453</i>	17.6 ± 1.50 ^{ab}	26.3 ± 1.33 ^a	31.3 ± 1.66 ^a	24.7 ± 2.08 ^{ab}	24.4 ± 1.88 ^{abc}
<i>ISRA454</i>	19.1 ± 0.99 ^{ab}	20.6 ± 0.45 ^b	25.9 ± 0.22 ^{cde}	22.0 ± 1.53 ^b	22.8 ± 1.04 ^{bc}
<i>ISRA519</i>	17.5 ± 0.71 ^{ab}	18.9 ± 0.48 ^b	27.0 ± 3.19 ^{bcd}	21.5 ± 0.71 ^b	24.3 ± 0.99 ^{abc}
<i>ISRA534</i>	17.5 ± 1.50 ^{ab}	21.8 ± 1.50 ^{ab}	29.4 ± 1.65 ^{abc}	26.4 ± 1.63 ^a	22.1 ± 2.66 ^{bc}
<i>ISRA538</i>	18.0 ± 1.08 ^{ab}	18.9 ± 1.15 ^b	28.4 ± 1.38 ^{abcd}	21.9 ± 1.84 ^b	26.8 ± 2.36 ^{ab}
<i>ORS3640</i>	17.3 ± 0.71 ^{ab}	21.6 ± 0.52 ^{ab}	28.5 ± 0.61 ^{abcd}	24.2 ± 2.69 ^{ab}	27.8 ± 0.51 ^a
<i>ORS3644</i>	17.4 ± 0.83 ^{ab}	22.8 ± 0.65 ^{ab}	30.1 ± 1.53 ^{ab}	22.4 ± 0.34 ^{ab}	24.3 ± 1.03 ^{abc}
<i>LMG9283</i>	17.7 ± 0.81 ^{ab}	22.6 ± 4.55 ^{ab}	24.9 ± 1.44 ^{de}	21.4 ± 1.92 ^b	22.3 ± 2.11 ^{bc}
<i>USD3187</i>	16.5 ± 0.00 ^b	21.6 ± 2.24 ^{ab}	28.6 ± 1.10 ^{abcd}	22.1 ± 0.97 ^b	21.9 ± 1.4 ^c
Control	17.7 ± 1.09 ^{ab}	23.0 ± 2.42 ^{ab}	22.3 ± 1.41 ^e	21.3 ± 2.43 ^b	20.1 ± 1.65 ^c
Mea ± sd	17.8 ± 1.13	21.6 ± 2.67	27.7 ± 2.81	22.7 ± 2.18	23.6 ± 2.62
CV (%)	5.574	9.101	5.759	7.587	7.554
P value	0.0446*	0.000385***	1.76e ⁻⁰⁷ ***	0.00258**	5.8e ⁻⁰⁵ ***

Significant codes: 0 '****', 0.001 '***', 0.01 '**', 0.05 '.', 0.1 ' ', 1 (significant differences according to Tukey test) ; ns (not significant difference) ; Mea ± sd (mean ± standard deviation) ; CV (coefficient of variation). In columns, means with identical superscript letters are statistically equivalent at the 5% probability level.

Table S4. Plant height (cm) of peanut cultivars at 45 days after planting under inoculation with *Bradyrhizobium* sp. Strains.

Treatments	Peanut cultivars				
	<i>Amoul Morom</i>	<i>Essamaay</i>	<i>55-437</i>	<i>Fleur 11</i>	<i>Sunu Gaal</i>
<i>ISRA400</i>	24.4 ± 0.63 ^a	26.0 ± 1.83 ^{bc}	32.5 ± 2.48 ^{abc}	26.8 ± 1.34 ^c	28.8 ± 1.95 ^{bcd}
<i>ISRA453</i>	24.8 ± 3.62 ^a	31.9 ± 1.72 ^a	38.8 ± 4.73 ^a	33.1 ± 0.95 ^a	32.9 ± 3.30 ^{ab}
<i>ISRA454</i>	24.6 ± 0.99 ^a	27.0 ± 1.15 ^{abc}	32.2 ± 1.39 ^{abc}	29.7 ± 1.57 ^{abc}	27.8 ± 1.55 ^{cd}
<i>ISRA519</i>	24.3 ± 1.19 ^{ab}	23.9 ± 0.85 ^c	33.2 ± 3.33 ^{ab}	27.4 ± 2.63 ^{bc}	32.9 ± 1.89 ^{ab}
<i>ISRA534</i>	23.6 ± 1.05 ^{ab}	28.9 ± 2.83 ^{abc}	37.5 ± 1.56 ^a	31.9 ± 1.25 ^{ab}	30.7 ± 2.96 ^{bcd}
<i>ISRA538</i>	23.7 ± 2.08 ^{ab}	27.9 ± 3.54 ^{abc}	34.9 ± 3.49 ^{ab}	29.5 ± 1.87 ^{abc}	36.0 ± 0.50 ^a
<i>ORS3640</i>	21.3 ± 0.85 ^{ab}	27.9 ± 1.21 ^{abc}	34.1 ± 1.38 ^{ab}	31.4 ± 2.50 ^{abc}	32.5 ± 1.68 ^{abc}
<i>ORS3644</i>	22.8 ± 0.33 ^{ab}	30.0 ± 2.94 ^{ab}	36.9 ± 4.23 ^{ab}	29.6 ± 1.91 ^{abc}	31.0 ± 2.00 ^{abcd}
<i>LMG9283</i>	21.9 ± 1.73 ^{ab}	28.1 ± 2.10 ^{abc}	30.5 ± 0.41 ^{bc}	28.5 ± 2.35 ^{abc}	27.9 ± 1.62 ^{cd}
<i>USD3187</i>	21.7 ± 1.08 ^{ab}	27.5 ± 2.65 ^{abc}	34.5 ± 2.13 ^{ab}	28.3 ± 3.06 ^{abc}	27.3 ± 1.43 ^d
Control	20.4 ± 0.74 ^b	25.1 ± 1.23 ^{bc}	26.4 ± 0.77 ^c	27.1 ± 1.84 ^{bc}	27.7 ± 1.08 ^{bcd}
Mea ± sd	23.1 ± 2.01	27.7 ± 2.87	33.8 ± 4.11	29.4 ± 2.66	30.4 ± 3.16
CV (%)	6.896	7.859	8.056	6.903	6.555
P value	0.00367**	0.000827***	1.86e ⁻⁰⁵ ***	0.00105**	6e ⁻⁰⁶ ***

Significant codes: 0 '****', 0.001 '***', 0.01 '**', 0.05 '.', 0.1 ' ', 1 (significant differences according to Tukey test); ns (not significant difference); Mea ± sd probability level. (mean ± standard deviation); CV (coefficient of variation). In columns, means with identical superscript letters are statistically equivalent at the 5%