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ENVIRONMENTAL MICROBIOLOGY - RESEARCH PAPER

Coinoculation impact on plant growth promotion: a review and meta-analysis on coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes

Glaciela Kaschuk[1] · André Carlos Auler[1] · Crislaine Emidio Vieira[1] · Felix Dapore Dakora[2] · Sanjay K. Jaiswal[2] · Sonia Purin da Cruz[3]

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Abstract

Coinoculation of symbiotic N_2-fixing rhizobia and plant growth-promoting *Bacillus* on legume seeds can increase crop productivity. We collected highly resolved data on coinoculation of rhizobia and bacilli on 11 grain legume crops: chickpea, common bean, cowpea, faba bean, groundnut, lentil, mung bean, pea, pigeon pea, soybean, and urad bean to verify the magnitude of additive effects of coinoculation in relation to single inoculation of rhizobia on plant growth and yield of grain legumes. Coinoculation of rhizobia and bacilli on legume seeds and/or soil during sowing significantly increased nodulation, nitrogenase activity, plant N and P contents, and shoot and root biomass, as well as the grain yield of most grain legumes studied. There were however a few instances where coinoculation decreased plant growth parameters. Therefore, coinoculation of rhizobia and *Bacillus* has the potential to increase the growth and productivity of grain legumes, and can be recommended as an environmental-friendly agricultural practice for increased crop yields.

Keywords Root growth · Plant nutrient content · Grain yield · Biological nitrogen fixation · Nodule

Introduction

Grain legumes play an important role in the diets of billions of people worldwide in both temperate and tropical regions, but are not always represented by high yields (Table 1). Most of them are either consumed directly as food by humans, or processed for use as fodder, biofuel, and other industrial purposes [1]. Legumes are highly valued crops because their seeds contain high levels of protein, fibre, mineral nutrients, lipids, and antioxidants due to their N_2-fixing ability, which supports high photosynthetic capacity [2, 3]. Additionally, the N-rich residues of legumes can improve soil fertility, thus contributing to increased food production in subsequent cropping cycles [1].

Legumes meet part of their N demand through N uptake from soil solution, and the other from symbiosis with rhizobia, which are gram-negative bacteria that elicit the formation of root nodules inside which bacteroids reduce N_2 to NH_3 in a process called biological N fixation (BNF) [6]. Although BNF can meet the full N requirements in legumes, it is often hampered by environmental conditions such drought, high temperatures, soil N, low efficiencies of rhizobial strains, and the type of plant species/cultivar [7, 8]. The

Responsible Editor: Luc F.M. Rouws

✉ Glaciela Kaschuk
glaciela.kaschuk@ufpr.br

André Carlos Auler
auler@ufpr.br

Crislaine Emidio Vieira
crislaine_emidio@hotmail.com

Felix Dapore Dakora
dakorafd@tut.ac.za

Sanjay K. Jaiswal
sanjaysiswa@gmail.com

Sonia Purin da Cruz
s.purin@ufsc.br

[1] Post-Graduation in Soil Science, Federal University of Paraná, Rua dos Funcionários, 1540, Curitiba, PR CEP 80035-050, Brazil

[2] Department of Chemistry, Tshwane University of Technology, Pretoria, South Africa

[3] Federal University of Santa Catarina, Campus Curitibanos, Rodovia Ulisses Gaboardi, km 3, Curitibanos, SC CEP 89520-000, Brazil

Table 1 Production of grain legume and cereal crops in the world during 2019

Grain legume	Production (million tonnes)	Area harvested (million ha)	Yield (kg ha^{-1})	Major producers
Chickpea	14.2	13.7	1038	India, 70%; Turkey, Russia, and Myanmar: 4% each
Common bean	28.9	33.1	874	India, 38%; Myanmar, 10%; Brazil, 8%
Cowpea	8.9	14.4	616	Nigeria, 40%; Niger, 27%; Burkina Faso, 7%
Faba bean	5.4	2.6	2108	China, 32%; Ethiopia, 19%; UK, 10%
Groundnut	48.8	29.6	1647	China, 36%; India, 14%; Nigeria, 9%
Lentil	5.7	4.8	1195	Canada, 38%; India, 21%; Australia, 9%
Mung bean	5.3	7.3	730	India, 30%; Myanmar, 30%; China, 16%
Pea	14.2	7.2	1979	Canada, 30%; Russia, 17%; China, 10%
Pigeon pea	4.4	5.6	788	India, 75%; Malawi, 10%; Myanmar, 8%
Soybean	333.7	120.5	2769	Brazil, 34%, USA, 29%; Argentina, 17%
Urad bean	n.e	n.e	909	India, 70%; Myanmar, Pakistan
Total legumes	469.9	238.8	n.e	

Data recalculated from FAO [4], except for mung bean, which was taken from World Vegetable Center [5]

n.e., not estimated

Legume species: chickpea, *Cicer arietinum*; common bean, *Phaseolus vulgaris*; cowpea, *Vigna unguiculata*; faba bean, *Vicia faba*; groundnut, *Arachis hypogaea*; lentil, *Lens culinaris*; mung bean, *Vigna radiata*; pea, *Pisum sativum*; pigeon pea, *Cajanus cajan*; soybean, *Glycine max*; urad bean, *Vigna mungo*

efficiency of BNF in legumes has been shown to increase with inoculation of efficient and competitive rhizobia that infect root hairs before indigenous soil rhizobia, which may be low N_2-fixers [6]. Inoculation of rhizobia at sowing allows bacteria to be present right at the beginning of root growth, thus favouring early nodule formation. In addition, seed inoculation promotes the formation of larger nodules, closer to the crown of the plant, resulting in nodular characteristics that provide greater symbiotic efficiency [6, 9].

Rhizobial inoculation is a common and highly recommended practice to improve crop yield, harvest index, and the protein content in grain legumes [3, 10, 11]. In many situations, efficient rhizobial inoculation meets all the legume's N requirements, and supports high grain yields [8, 12, 13]. However, BNF efficiency could be improved by coinoculation of rhizobia with plant growth-promoting bacteria (PGPB), which enhance rhizobial symbiosis by complementary mechanisms in plant growth promotion [10, 13, 14].

Among PGPB, gram-positive bacteria of the *Bacillus* genus caught the attention of researchers to the various mechanisms by which they promote plant growth [11, 15, 16], as well as their resilience through the formation of endospores, which increases their chance of success as bacterial inoculants [17]. *Bacillus* and other related genera are potential PGPB due to their ability to produce phytohormones such as gibberellic acid (GA) and indole-3-acetic acid (IAA) [11, 15, 16, 18–20]. In addition, *Bacillus* strains are also considered phosphate-solubilizing bacteria due to their ability to release large amounts of siderophores (which solubilizes Fe from the inorganic mineral $FePO_4$), organic acids (which decrease soil solution pH, and dissolve more labile inorganic phosphate), and phosphatases (which mineralize organic phosphates present in soil organic matter) [11, 15, 16, 19, 21, 22]. Some *Bacillus* strains produce potent toxins which act as antifungal and antibiotic compounds that control growth of antagonistic microorganisms, or induce plant resistance against pathogens [15, 16, 23–30]. *Bacillus* strains also release ACC deaminase, an enzyme that degrades the precursor of ethylene, a phytohormone that induces plant senescence [16] and alleviates drought stress [31]. Due to these traits, there are several inoculant products based on *Bacillus* species which are available in the market and can be used for agricultural crops [15, 17]. These inoculants (rhizobia and bacilli) can be coinoculated in grain legumes to increase the symbiotic efficiency of rhizobia through complementary mechanisms of plant growth promotion [11, 32, 33]. That way, coinoculation could also increase the symbiotic efficiency of rhizobia, legume N content, plant size, and grain yields. The main objective of this study was to assess the magnitude of additive effects of coinoculation of rhizobia and bacilli relative to single inoculation of rhizobia on plant growth and yield of grain legumes.

Materials and methods

Data collection

Data were acquired from a library search of peer-reviewed articles in the platforms "Web of Science" and "Google Scholar", using the keywords: "coinoculation", "rhizobium"

Table 2 Log response ratio of nodule and biological N fixation due to the coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes

Grain legume	Exp. condition	Nodulation				Nitrogenase activity			
		n	*lr*	*95% C.I*	*p*	*n*	*lr*	*95% C.I*	*p*
Chickpea	Pot	97	0.131	0.071; 0.192	< 0.0001	50	0.146	0.039; 0.253	0.0074
	Field	94	0.260	0.220; 0.299	< 0.0001	4	0.134	0.050; 0.214	< 0.0001
Common bean	Pot	152	0.092	0.033; 0.151	0.0023	33	0.197	0.099; 0.294	< 0.0001
	Field	18	0.020	− 0.046; 0.085	0.5546	4	0.139	− 0.296; 0.574	0.5321
Cowpea	Pot	159	0.013	− 0.032; 0.057	0.5749				
	Field	4	− 0.337	− 0.609; − 0.064	0.0154				
Faba bean	Field	138	0.029	− 0.020; 0.077	0.2457	21	0.299	0.164; 0.433	< 0.0001
Groundnut	Pot	27	0.594	0.454; 0.734	< 0.0001	7	0.099	− 0.052; 0.251	0.1961
Lentil	Pot	12	0.301	0.2165; 0.385	< 0.0001	1	− 0.569	− 0.997; − 0.142	0.0090
	Field	8	0.095	0.021; 0.169	0.0121	2	0.475	0.331; 0.619	< 0.0001
Mung bean	Pot	72	0.006	− 0.064; 0.077	0.8651	48	− 0.211	− 0.322; − 0.102	0.0002
	Field	30	0.199	0.165; 0.232	< 0.0001				
Pea	Pot	8	0.226	0.002; 0.452	0.0485	2	− 0.376	− 0.758; 0.005	0.0532
Pigeon pea	Pot	25	0.100	− 0.111; 0.311	0.3520	1	0.291	0.139; 0.442	0.0002
	Field	21	0.223	− 0.158; 0.611	0.2483				
Soybean	Pot	96	0.213	0.142; 0.283	< 0.0001	47	0.045	− 0.156; 0.246	< 0.0001
	Field	89	0.400	0.300; 0.501	< 0.0001	4	− 0.114	− 0.723; 0.495	0.7129
Urad bean	Pot	6	0.036	− 0.072; 0.144	0.5100				

n is the number of observations; *lr* is the log response ratio obtained by dividing treatment value (rhizobia + bacilli) per control (rhizobia); 95% C.I. are the lower and upper confidence intervals at $p < 0.95$

Interpretation: Negative values of *lr* indicated that coinoculation of rhizobia and bacilli decreases the variable values, and positive values of *lr* indicated that coinoculation promoted increases in the variable values. When the value of *lr* is negative and both confidence intervals are negative, the effects are significantly negative. When the value of *lr* is positive and both confidence intervals are positive, the effects are significantly positive

Legume species: chickpea, *Cicer arietinum*; common bean, *Phaseolus vulgaris*; cowpea, *Vigna unguiculata*; faba bean, *Vicia faba*; groundnut, *Arachis hypogaea*; lentil, *Lens culinaris*; mung bean, *Vigna radiata*; Pea, *Pisum sativum*; pigeon pea, *Cajanus cajan*; soybean, *Glycine max*; urad bean, *Vigna mungo*

Database and the "R" script for the meta-analysis are presented in the Supplementary Material

or "rhizobia" and "bacillus" or "bacilli", associated with one of the grain legumes listed below in pots or field experiments. The outcome of the library search (Supplementary Material) for each grain legume in this meta-analysis included chickpea (*Cicer arietinum*) [22, 34–49]; common bean (*Phaseolus vulgaris*) [18, 23, 24, 30, 31, 50–65]; cowpea (*Vigna unguiculata*) [66–72]; faba bean (*Vicia faba*) [21, 73–76]; groundnut (*Arachis hypogaea*) [25, 27, 28, 77–79]; lentil (*Lens culinaris*) [26, 80–84]; mung bean (*Vigna radiata*) [85–91]; pea (*Pisum sativum*) [65, 83, 92]; pigeon pea (*Cajanus cajan*) [93–96]; soybean (*Glycine max*) [20, 51, 65, 84, 97–115]; and urad bean (*Vigna mungo*) [14, 116].

In the meta-analysis, plants or plots inoculated only with one rhizobial strain were considered as "control", and coinoculation with at least one rhizobium and one bacillus strain as "treatment". *Paenibacillus*, *Brevibacillus*, and *Lysinibacillus*, which have been recognized as plant growth-promoting *Bacillus* bacteria, were used by some researchers in their experiments.

Statistical parameters such as the mean, standard deviation, and number of replications of each experimental unit were obtained for the following variables: nodules (number and/or dry matter), biological nitrogen fixation (BNF; nitrogenase activity or N-derived from BNF by N^{15}), N accumulated in the plant (N concentration or total mass in the plant, or in the shoot), P accumulated in the plant (P concentration or total mass in the plant, grain, or in the shoot), root size (length or dry matter), shoot size (height or dry matter), and grain yield (dry matter of grains). Studies with less than three replications were excluded from the meta-analysis. When standard deviation was not presented in articles, it was calculated based on coefficient of variation or standard error. If none of these indicators were presented, we first calculated coefficient of variation with the means available in each experiment and then obtained standard deviation values.

Table 3 Log response ratio of the coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes

Grain legume	Exp. condition	Plant N				Plant P			
		n	*lr*	*95% C.I*	*p*	*n*	*lr*	*95% C.I*	*p*
Chickpea	Pot	28	0.311	0.185; 0.436	< 0.0001	12	0.165	0.112; 0.218	< 0.0001
	Field	23	0.051	0.012; 0.089	0.0095	26	0.222	0.168; 0.277	< 0.0001
Common bean	Pot	20	0.041	−0.105; 0.187	0.5825				
	Field	7	0.179	0.103; 0.255	< 0.0001				
Cowpea	Pot	90	−0.185	−0.228; −0.143	< 0.0001				
	Field	2	−0.055	−0.255; 0.144	0.5877				
Faba bean	Field	24	0.072	0.011; 0.132	0.0200	18	0.050	−0.002; 0.102	0.0604
Groundnut	Pot	2	−0.077	−0.587; 0.435	0.7691	6	−0.022	−0.059; 0.015	0.2458
Lentil	Field					2	0.244	0.054; 0.435	0.0120
Mung bean	Pot	72	0.215	0.177; 0.253	< 0.0001				
	Field	12	0.136	0.071; 0.202	< 0.0001				
Pea	Pot	4	0.030	−0.051; 0.119	0.4326				
Pigeon pea	Pot	1	0.117	0.043; 0.190	0.0019				
	Field	10	−0.003	−0.120; 0.113	0.9555				
Soybean	Pot	5	0.458	0.032; 0.883	0.0349				
	Field	50	−0.046	−0.082; −0.011	0.0097	2	0.000	−0.015; 0.015	0.9900
Urad bean	Pot	2	0.019	−0.008; 0.047	0.1739	4	0.091	0.058; 0.124	< 0.0001

n is the number of observations; *lr* is the log response ratio obtained by dividing treatment value (rhizobia + bacilli) per control (rhizobia); 95% C.I. are the lower and upper confidence intervals at $p < 0.95$

Interpretation: Negative values of *lr* indicated that coinoculation of rhizobia and bacilli decreases the variable values, and positive values of *lr* indicated that coinoculation promoted increases in the variable values. When the value of *lr* is negative and both confidence intervals are negative, the effects are significantly negative. When the value of *lr* is positive and both confidence intervals are positive, the effects are significantly positive

Legume species: chickpea, *Cicer arietinum*; common bean, *Phaseolus vulgaris*; cowpea, *Vigna unguiculata*; faba bean, *Vicia faba*; groundnut, *Arachis hypogaea*; lentil, *Lens culinaris*; mung bean, *Vigna radiata*; pea, *Pisum sativum*; pigeon pea, *Cajanus cajan*; soybean, *Glycine max*; urad bean, *Vigna mungo*

Database and the "R" script for the meta-analysis are presented in the Supplementary Material

Effect size was calculated using the log response ratios (*lr*) and the total variability in the response ratios, from control to experimental groups, with equations proposed by Hedges et al. [117] and Gurevitch and Hedges [118]. Analyses were done at R platform version 4.0.1 (R Core Team, 2020) using metaphor package [119]; script for run is presented as Supplementary Material.

Results

Overall, the meta-analysis indicated that coinoculation of rhizobia and bacilli promoted plant growth of different grain legumes relative to single rhizobia inoculation. Nodulation (or nodule) was the most responsive variable to coinoculation, but other plant variables were also highly increased. In pot experiments, coinoculation significantly increased nodulation of chickpea, common bean, groundnut, lentil, pea, and soybean, while in field experiments, it increased nodulation of chickpea, cowpea, mung bean, and soybean (Table 2). In field-grown cowpea, coinoculation decreased the number and mass of nodules (Table 2). In the other legumes, the coinoculation of rhizobia and bacilli did not change nodulation (Table 2).

Nitrogenase activity (indicator of BNF) was stimulated by coinoculation in chickpea, common bean, and pigeon pea in pot experiments, and in faba bean and lentil in field experiments. However, it was decreased in lentil (n = number of data points = 1) and mung bean ($n = 48$) in pot experiments (Table 2). Biological N fixation of other grain legumes was not affected by coinoculation of rhizobia with bacilli (Table 2).

Most grain legumes accumulated more N in the plant when coinoculated, i.e., chickpea (pot and field), common bean (field), faba bean (field), mung bean (pot and field), pigeon pea (pot), and soybeans (pot). On the other hand, the plant N content of soybean and cowpea in the field was negatively affected by coinoculation (Table 3). Likewise, coinoculation promoted higher uptake of P in the chickpea (pot and field), lentil (field), and urad bean (pot) (Table 3).

Coinoculation promoted shoot and root growth of most grain legumes. Chickpea (pot and field), faba bean (field), groundnut

Table 4 Log response ratio of the coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes

Grain legume	Exp. condition	Root size				Shoot size			
		n	*Log R*	*95% C.I*	*p*	*n*	*Log R*	*95% C.I*	*p*
Chickpea	Pot	33	0.341	0.156; 0.523	0.0003	67	0.312	0.182; 0.440	< 0.0001
	Field	16	0.179	0.120; 0.238	< 0.0001	71	0.184	0.123; 0.244	< 0.0001
Common bean	Pot	38	0.007	− 0.039; 0.053	0.7604	122	0.054	0.005; 0.103	0.0312
	Field	6	− 0.097	− 0.192; − 0.003	0.0442	20	0.071	0.025; 0.118	0.0025
Cowpea	Pot	158	− 0.015	− 0.050; 0.021	0.4127	116	− 0.070	− 0.097; − 0.043	< 0.0001
	Field					2	− 0.034	− 0.239; 0.171	0.7455
Faba bean	Pot					4	0.033	− 0.032; 0.097	0.3213
	Field	80	0.094	0.043; 0.145	0.0003	104	0.034	0.006; 0.062	0.0167
Groundnut	Pot	37	0.177	0.123; 0.230	< 0.0001	72	0.119	0.057; 0.181	0.0002
Lentil	Pot	8	0.170	0.111; 0.229	< 0.0001	20	0.031	0.020; 0.042	< 0.0001
	Field					5	0.056	− 0.0201; 0.132	0.1494
Mung bean	Pot	18	0.206	− 0.009; 0.421	0.0605	80	0.151	0.065; 0.237	0.0006
	Field					24	0.129	0.072; 0.186	< 0.0001
Pea	Pot	12	0.040	− 0.017; 0.097	0.1716	13	0.043	− 0.019; 0.105	0.1729
Pigeon pea	Pot	1	0.388	− 0.145; 0.920	0.1533	17	0.095	− 0.052; 0.242	0.2043
	Field	11	0.006	− 0.105; 0.117	0.9202	15	0.065	− 0.039; 0.170	0.2217
Soybean	Pot	42	0.237	0.161; 0.314	< 0.0001	58	0.181	0.122; 0.240	< 0.0001
	Field	19	0.198	0.131; 0.264	< 0.0001	45	0.055	0.032; 0.077	< 0.0001
Urad bean	Pot	7	0.058	− 0.019; 0.136	0.1416	8	0.063	0.002; 0.123	0.0427

n is the number of observations; *lr* is the log response ratio obtained by dividing treatment value (rhizobia + bacilli) per control (rhizobia); 95% C.I. are the lower and upper confidence intervals at $p < 0.95$

Interpretation: Negative values of *lr* indicated that coinoculation of rhizobia and bacilli decreases the variable values, and positive values of *lr* indicated that coinoculation promoted increases in the variable values. When the value of *lr* is negative and both confidence intervals are negative, the effects are significantly negative. When the value of *lr* is positive and both confidence intervals are positive, the effects are significantly positive

Legume species: chickpea, *Cicer arietinum*; common bean, *Phaseolus vulgaris*; cowpea, *Vigna unguiculata*; faba bean, *Vicia faba*; groundnut, *Arachis hypogaea*; lentil, *Lens culinaris*; mung bean, *Vigna radiata*; pea, *Pisum sativum*; pigeon pea, *Cajanus cajan*; soybean, *Glycine max*; urad bean, *Vigna mungo*

Database and the "R" script for the meta-analysis are presented in the Supplementary Material

(pot), lentil (pot), and soybean (pot and field) had larger roots, while only common bean (field) had smaller roots because of coinoculation (Table 4). In addition, there were significant increases in shoot size of chickpea (pot and field), common bean (pot and field), faba bean (field) groundnut (pot), lentil (pot), mung beans (pot and field), soybean (pot and field), and urad bean (pot), and only decreased in cowpea (pot) (Table 4).

Finally, coinoculation had positive effects on grain yield of chickpea (pot and field), cowpea (pot), faba bean (field), lentil (field), mung bean (field), and soybean (pot) (Table 5). Nevertheless, negative effects were observed on lentil grown in pot ($n = 1$) (Table 5).

Discussion

During several decades, researchers have hypothesized that inoculation of more than one type of microorganism can increase the population of microorganisms that act in plant ecophysiology by complementary beneficial mechanisms [10, 11, 32, 33]. In the present meta-analysis of data regarding coinoculation of rhizobia with bacilli in 11 grain legume crops, we produced information that corroborates to the above said hypothesis. Our findings expand the current knowledge of inoculation techniques to the other legumes that were previously applied for soybean only [13, 14]. This is the first study worldwide on meta-analysis related to coinoculation of grain legumes with rhizobia and bacilli, and it emphasizes the role of several strains of the *Bacillus* genus to improve rhizobial symbiosis performance, and increase growth and yields of grain legumes in different parts of the world (cf. Supplementary Material).

Our meta-analysis confirmed that coinoculation of rhizobia and bacilli enhances the root nodule number, accumulates more N and P, increases root and shoot growth, and finally results in higher grain yields (Tables 2, 3, 4, and 5). Higher nodulation and increased root growth may have been consequence of increased phytohormone production, such as

Table 5 Log response ratio of the coinoculation of rhizobia and plant growth-promoting bacilli in grain legumes

Grain legume	Exp. condition	Grain yield			
		n	*Log R*	*95% C.I*	*p*
Chickpea	Pot	2	0.161	0.007; 0.316	0.0405
	Field	34	0.159	0.096; 0.221	< 0.0001
Common bean	Pot	1	− 0.215	− 0.712; 0.282	0.3963
	Field	20	0.060	− 0.027; 0.146	0.1756
Cowpea	Pot	3	0.261	0.210; 0.313	< 0.0001
Faba bean	Field	53	0.058	0.014; 0.103	0.0105
	Pot	1	0.237	− 0.980; 1.454	0.7028
Lentil	Pot	1	− 0.150	− 0.236; − 0.036	0.0007
	Field	3	0.079	0.015; 0.144	0.0164
Mung bean	Pot	18	− 0.113	− 0.308; 0.083	0.2591
	Field	9	0.181	0.109; 0.252	< 0.0001
Pigeon pea	Pot	1	− 0.259	− 0.972; 0.454	0.4760
Soybean	Pot	3	0.119	0.064; 0.174	< 0.0001
	Field	52	− 0.005	− 0.026; 0.017	0.6643
Urad bean	Pot	2	0.033	− 0.064; 0.130	0.5082

n is the number of observations; *lr* is the log response ratio obtained by dividing treatment value (rhizobia + bacilli) per control (rhizobia); 95% C.I. are the lower and upper confidence intervals at $p < 0.95$

Interpretation: Negative values of *lr* indicated that coinoculation of rhizobia and bacilli decreases the variable values, and positive values of *lr* indicated that coinoculation promoted increases in the variable values. When the value of *lr* is negative and both confidence intervals are negative, the effects are significantly negative. When the value of *lr* is positive and both confidence intervals are positive, the effects are significantly positive

Legume species: chickpea, *Cicer arietinum*; common bean, *Phaseolus vulgaris*; cowpea, *Vigna unguiculata*; faba bean, *Vicia faba*; groundnut, *Arachis hypogaea*; lentil, *Lens culinaris*; mung bean, *Vigna radiata*; pea, *Pisum sativum*; pigeon pea, *Cajanus cajan*; soybean, *Glycine max*; urad bean, *Vigna mungo*

Database and the "R" script for the meta-analysis are presented in the Supplementary Material

gibberellic acid (GA) and indole-3-acetic acid (IAA), which stimulate plant cell division and elongation [120]. In fact, many studies that compose the database of this meta-analysis have indicated that *Bacillus* strains produce IAA and other plant growth-promoting substances [18–20, 44–47, 49, 56, 79, 84–86, 88, 98, 108].

Coinoculated legumes accumulated more N in relation to control (plants inoculated only with rhizobia) (Table 3). Higher N content may have been consequence of higher nodulation since nodule dry mass and BNF were positively highly correlated (e.g., [14]). However, it is interesting to mention that although coinoculation increased plant N content in the majority of grain legumes, it did not necessarily increase nitrogenase activity of rhizobial nodules (Table 2). It could be that increased N accumulation in legume plants was related to increased root growth and as increased root growth ensures that plants were supplied with more nutrients [121]. Therefore, high N uptake (Table 3) was probably the result of both increased nodule N fixation capacity (Table 2) and the ability of bacilli to promote root growth (Table 4).

Moreover, coinoculation of rhizobia and bacilli in grain legumes also enhanced the level of P accumulation in the plants (Table 3), the result of the combined effect of high root growth and P solubilization activity of *Bacillus* spp. [15, 92, 100, 121]. Many reports which were used in this meta-analysis confirmed the capacity of *Bacillus* strains to solubilize P in growth media and in soil used for the cultivation of inoculated legumes [19, 34, 38, 44, 49, 78, 79, 91]. In addition to the above results, shoot and root biomasses of chickpeas and soybeans were increased by the rhizobia-bacilli coinoculation and suggested that root growth provides more resources for shoot growth (Table 3).

Additionally, increases in root size can also be very beneficial under stressful conditions because higher root systems can uptake more water and nutrients [85, 122, 123]. For example, coinoculation of *Rhizobium tropici* with *Paenibacillus polymyxa* alleviated the negative effects of severe drought stress on common beans under greenhouse conditions [31]. Likewise, coinoculation of *Mesorhizobium ciceri* with *Bacillus* sp. increased chickpea growth and grain yields in P-deficient soil in dry areas of a Mediterranean region [22]. The results in Table 5 are consistent with this proposition, as several legume crops produced more grains when they were coinoculated.

Some legumes had more pronounced responses than others. For example, the most consistent positive results were obtained with chickpea and soybean, whereas cowpea had some negative responses, particularly in the plant N contents (Table 2) and shoot size (Table 3). Regarding chickpea and soybean, increase in shoot size (Table 4) resulted in high grain yields (Table 5). However, in cowpea, coinoculation decreased shoot growth (negative *lr* for shoot size) but increased grain yield (positive *lr* for grain yield). Results corroborate with the fact that the benefits of coinoculation were not related to increased shoot growth proportionally with grain yield, but probably to changes in the source-sink relationships and in the harvest index of these legume crops [3].

In soils, both rhizobia and bacilli biofilms consume recently produced photosynthates. Rhizobia symbiosis may consume as much as 14% of recent photosynthates [2] while rhizospheric and soil microorganisms may absorb 6 to 10% of photosynthates exuded through roots [124]. This amount should not compromise plant growth because photosynthetic rates are likely to increase due to C sink stimulation [2, 3, 125]. On the contrary, complementary characteristics of rhizobia-bacilli-legume tripartite association should result in higher plant growth and grain yield. In addition to the plant growth-promoting mechanisms related to phytohormone up-regulation and P solubilization, *Bacillus* spp. also play an important role on the biological control of phytopathogen fungi and invertebrate plagues. Indeed, many studies used for this meta-analysis were designed to test the efficacy of *Bacillus* strains to control plagues and diseases that affect grain legume growth [25–28, 30, 60, 76, 80, 92].

Coinoculation of rhizobia and bacilli is possibly a step forward in the "Green Revolution" headed by microbial inoculants [126]. In this meta-analysis, we gathered results involving several different bacilli and rhizobia strains in many legume crops worldwide. The results confirmed that coinoculation of rhizobia and bacilli strains was a general strategy to increase biological nitrogen fixation, plant growth, and nutrient acquisition of nearly all grain legumes tested. Therefore, this meta-analysis shows that coinoculation could be considered a viable technology for grain legumes in general, which suggests that more studies involving the best combinations of rhizobia and bacilli in each grain legume crop should be pursued.

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Author contribution Glaciela Kaschuk and Crislaine Emidio Vieira compiled the data; André Carlos Auler performed the statistical analyses; all authors contributed to the interpretation of the data and writing and editing the manuscript; all authors have approved the version to be published, and have agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy or integrity of any part of the work are appropriately investigated and resolved.

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Declarations

Conflict of interest The authors declare no competing interests.

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