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Biological seed treatments promote crop establishment and yield: a global meta-analysis

Jay Ram Lamichhane¹ · David Camilo Corrales¹ · Elias Soltani²

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Abstract

Seeds are a vector of genetic progress and, as such, they play a significant role in the sustainability of the agri-food system. The current global seed market is worth USD 60 billion that is expected to reach USD 80 billion by 2025. Seeds are most often treated before their planting with both chemical and biological agents/products to secure good seed quality and high yield by reducing or preventing losses caused by diseases. There is increasing interest in biological seed treatments as alternatives to chemical seed treatments as the latter have several negative human health and environmental impacts. However, no study has yet quantified the effectiveness of biological seed treatments to enhance crop performance and yield. Our meta-analysis encompassing 396 studies worldwide reveals for the first time that biological seed treatments significantly improve seed germination (7±6%), seedling emergence (91±5%), plant biomass (53±5%), disease control (55±1%), and crop yield (21±2%) compared to untreated seeds across contrasted crop groups, target pathogens, climatic regions, and experimental conditions. We conclude that biological seed treatments may represent a sustainable solution to feed the increasing global populations while avoiding negative effects on human health and ensuring environmental sustainability.

Keywords Non-chemical seed treatment · Seed germination · Seedling emergence · Soil-borne pathogens · Sustainability

1 Introduction

Crop losses due to pests (*sensu lato* that includes animal pests, pathogens, and weeds) may range from 50 to more than 80% (Oerke 2006) and those caused by crop pathogens alone cost the global economy USD220 billion annually (Savary et al. 2019). These losses may be prevented or contained by applying effective crop protection measures. Chemical pesticides are the most commonly used crop protection measures, from pre-sowing to post-harvesting (Oerke 2006; Cooper and Dobson 2007; Aktar et al. 2009). More specifically to seed treatments, chemical seed treatments are generally aimed at controlling seed- and soil-borne pests affecting crop establishment (Figure 1), crop biomass development, and yields (Wrather et al. 2010; Simpson et al. 2011; Munkvold et al. 2014; Sappington et al. 2018; Lamichhane et al. 2020b; Hitaj et al. 2020).

The routine-based planting of chemically treated seeds has raised several socio-economic, human health, and environmental concerns. This is because of the poor efficacy or inconsistent effectiveness of chemical seed treatments in controlling seed- and soil-borne pests (Rossman et al. 2018; Mourtzinis et al. 2019; Lundin et al. 2020; You et al. 2020; Fadel Sartori et al. 2020); risk exposure to operators that treat seeds or handle treated seeds (White and Hoppin 2004; Han et al. 2021); development of different forms of human cancer (AGRICAN 2020); and negative effects on non-target organisms such as bees (Rundlof et al. 2015; Main et al. 2020), birds (Li et al. 2020b; Fernández-Vizcaíno et al. 2021), and soil beneficial microorganisms (Nettles et al. 2016; Zaller et al. 2016; Gomes et al. 2017). In addition, the planting of chemically treated seeds negatively affects beneficial plant fungal endophytes, involved in plant growth and development thereby reducing early plant growth (Vasanthakumari et al. 2019).

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Fig. 1 Damping-off and root rot of soybean caused by *Pythium* spp. Poor seedling emergence and post-emergence seedling death leading to a low quality of crop establishment and stand development are an indicator of these diseases. Seed treatments represent an important practice to protect the seed and seedlings both pre- and post-emergence. In fields with historical problems of soil-borne pathogens, seed treatments represent an important agronomic lever to enhance germination and emergence vigor (i.e., the speed of seed germination and seedling emergence) that is essential for plant development and yield. Photo courtesy of Tom Allen, Mississippi State University, USA.

Therefore, there is a need to limit or replace chemical seed treatments with other sustainable practices to achieve the same goal — viz. improved seed germination, seedling emergence, biomass production, pest control, and crop yield — with no or reduced human health and environmental impacts (Lamichhane 2020).

Biological seed treatments contain active ingredients encompassing microbes like fungi and bacteria, as well as plant and algae extracts. Previous studies investigated the effectiveness of biological seed treatments in controlling seed- and soil-borne pests including their potential to improve seed germination, seedling emergence, plant biomass development, and yield (see the list of references used in the meta-analysis). However, the type of product used for biological seed treatments, the target seed- and soil-borne pests, the climate zone, the crop group, and the experimental conditions considered in these studies are very heterogeneous. Consequently, the effectiveness of a given biological seed treatment may significantly vary across contrasted systems or conditions and, therefore, the results of individual studies are not sufficient to draw a general conclusion. Quantitative systematic review or meta-analysis is particularly useful in quantifying and synthesizing the potential of biological seed treatments on crop development and yield. Enhanced knowledge on the best performing biological seed treatments across different crop species or different environmental gradients will be instrumental in the adoption of planting biologically treated seeds. This will in turn save yields needed to feed the increasing world population while reducing environmental risk and health hazards. Several recent meta-analyses in the field of agronomy successfully quantified the impact of different

cropping practices on crop development and yield (Soltani and Soltani 2015; Carrillo-Reche et al. 2018; Knapp and van der Heijden 2018; Li et al. 2020a, c). In contrast, to the best of our knowledge, no meta-analysis has been performed yet to quantify the effectiveness biological seed treatments on crop performance and yield.

The objective of this study was to quantify, via a meta-analysis, the effectiveness of biological seed treatments in improving seed germination, seedling emergence, plant biomass development, disease control, and yield compared to untreated seeds (i.e., without application of any chemical or biological products) across contrasted environmental conditions, crop groups, and climate zones.

2 Materials and methods

2.1 Data sources

Data for the meta-analysis were retrieved from the ISI-Web of Science database taking into account articles published before 11 June 2020. The keywords used to find the articles were “non-chemical seed treatment” (68 publications), “biological seed treatment” (140 publications), “seed bacterization (366 publications), and “seed treatment” (3284 publications). Only the studies that compared biological seed treatments vs. untreated seeds and their effect on the following five variables — viz. seed germination (SG), seedling emergence (SE), plant biomass (PB), disease control (DC; either disease incidence or severity) or crop yield (CY) — were included in the meta-analysis. Although CY is the key final output of interest, we also focused on other four response variables for two main reasons. First, given that we included all crop groups in our meta-analysis, the definition of the response variable CY differs between cereals (the quantity of the harvested grain per unit surface) and vegetables (the quantity of the harvested biomass per unit surface that could be sprouts or leaves used such as ready-to-use leafy vegetables). Second, the potential of biological seed treatments to improve crop performance is mainly due to an improved control of seed- and soil-borne pests that affect the early crop development phase (SG & SE etc).

We did not consider those studies where seed treatments were applied to break seed dormancy or to control weeds. Conference papers or book series were also excluded especially if they were not available online or did not contain a full text. Overall, 64 articles were selected for seed germination, 126 articles for seedling emergence, 153 articles for plant biomass, 210 articles for disease development, and 163 articles for crop yield (Supplementary Data 3). The mean values and the number of replications/observations for the selected characteristics were extracted from the selected articles. For studies that consisted of a series of experiments, different biological seed treatments or different environmental

conditions, each comparison between biological seed treatments and the control treatments was considered as a separate data point ("observation").

2.2 Data set overview

The selected articles contained 8596 observations. Most of these articles tested biological seed treatments under several sets of experiments and had a high weighted data. DC was investigated in about 34.5% of the total observations followed by SE (24.6%), PB (17.6%), CY (14.6%), and SG (8.8%).

Experiments were conducted either under controlled or field conditions. Experiments performed under controlled conditions included those on SG and PB measurements. SE data were measured either in studies conducted under controlled conditions (48% of data) or those carried out under field conditions (52% of data). Likewise, 42% and 58% of the data on DC were measured under controlled and field conditions, respectively. Most of the data on CY were obtained under field conditions (82%) while the rest (18%) were collected under controlled conditions. Field experiments were conducted across South and North America, Europe, North Africa and Asia under different climate zones. Key information concerning crop or crop group, the target biotic stress, and the measured variables are presented in Supplementary Data 3.

In the selected articles for meta-analysis, plant pathogenic fungi were the key target of biological seed treatments (58%) followed by oomycetes (11%), bacteria (8%), nematodes (3%), and viruses (3%). Some studies also considered a pathogen complex that involved more than one pathogen at the same time (e.g., under field conditions) which included 13% of the data. In experiments conducted under controlled conditions, seeds/soils were either artificially inoculated or not with one or more pathogens. Non-inoculated treatments (i.e., control) were also considered which contained 4% of the data. We did not consider the potential effect of biological seed treatments on insect pest control as only little information is available on this topic in the literature.

2.3 Data analysis

In each study and for each data point, the response ratio (R) was calculated to detect the effects of biological seed treatments on the five response variables as follows (Marty and BassiriRad 2014):

$$R = \left(\frac{\bar{X}_t}{\bar{X}_c} \right) \quad (1)$$

where \bar{X}_t and \bar{X}_c are the mean values for measured plant traits subjected to biological seed treatments and control (untreated

seeds), respectively. Standard error (SE) was estimated for each n observations as shown below (Neyeloff et al. 2012):

$$SE = \frac{R}{\sqrt{R \times n}} \quad (2)$$

The weighted average has a desirable feature as it gives more weight for studies with a higher number of observations compared with those with a lower number of observations. This provides an appropriate way to calculate the overall effect size (Gurevitch and Hedges 1999). The weight for each observation (w_v) was calculated as below:

$$w_v = \frac{1}{(SE^2 + v)} \quad (3)$$

where v is a constant that represents variability due to sampling error as well as variability in the population of effects and can be calculated as follows (Neyeloff et al. 2012):

$$v = \frac{Q - (k - 1)}{\sum w - \left(\frac{\sum w^2}{\sum w} \right)} \quad (4)$$

where k is number of observations, w is equal to $\frac{1}{SE^2}$ and Q is heterogeneity among observations (see the section 2.4 for its calculation).

Weighted average of the response ratio (\bar{R}) was calculated as follows (Neyeloff et al. 2012):

$$\bar{R} = \frac{\sum (w_v \times R)}{\sum w_v} \quad (5)$$

Heat map graphs were used to show the differences among study factors for \bar{R} . The weighted average of the response ratio >1 in the heat map indicates a positive response while a value of <1 shows a negative response. Standard error of \bar{R} ($SE_{\bar{R}}$) was estimated as shown below (Neyeloff et al. 2012) :

$$SE_{\bar{R}} = \sqrt{\frac{1}{\sum w_v}} \quad (6)$$

Significant changes were tested by 95% confidence intervals (CI), which were calculated as follows (Neyeloff et al. 2012):

$$CI = \bar{R} \pm 1.96 \times SE_{\bar{R}} \quad (7)$$

No overlap of confidence intervals with zero indicates that biological seed treatments significantly affected the measured plant traits.

For easier interpretation of the results, the percentage of change due to biological seed treatments compared with the control was calculated (changes (%)) for all the measured

plant traits as follows (Hedges et al. 1999; Marty and BassiriRad 2014; Soltani et al. 2018):

$$\text{Changes (\%)} = \left[\bar{R} - 1 \right] \times 100 \quad (8)$$

where a positive and a negative percentage change value indicates an increase and a decrease of the measured trait, respectively. For example, for disease development, a negative value shows a reduction in disease development (i.e., a better disease control).

2.4 Heterogeneity test

The heterogeneity among the effect sizes of studies was tested using a chi square (Q) test and I^2 statistic to determine whether the variance among effect sizes was significantly greater than the expected sampling error (Rosenberg et al. 2004). A significant Q value shows that a portion of the heterogeneity can be explained by subgrouping the studies into different categories (Traveset and Verdu 2002; Rosenberg et al. 2004; Soltani et al. 2018). Both fixed- and random-effects were calculated to determine the heterogeneity in different studies (Neyeloff et al. 2012). However, a random-effect is more suitable than a fixed-effect in our meta-analysis. This is because the data used came from a series of individual studies that were performed across different crop groups, biological seed treatment types, and climate zones. Therefore, it is unlikely that all the studies were functionally equivalent. Therefore, Q values were calculated as follows (Neyeloff et al. 2012):

$$Q = \sum (w \times R^2) - \frac{[\sum (w \times R)]^2}{\sum w} \quad (9)$$

The calculated Q shows random-effects (Q_v) if we use w_v instead of w in Eq. (9). Finally, I^2 statistics were calculated as suggested previously (Neyeloff et al. 2012):

$$I^2 = \frac{(Q - df)}{Q} \quad (10)$$

where I^2 indicates the heterogeneity due to the random-effects if we use Q_v and df is equal to $k-1$. I^2 ranges between 0 and 100%. The heterogeneity is not important when $I^2 < 40\%$, moderate when $30\% < I^2 < 60\%$, substantial when $50\% < I^2 < 90\%$, and considerable when $75\% < I^2 < 100\%$.

2.5 Mean effect size by study factor

Study factors were categorized into six different subgroups to further investigate the effect of biological seed treatments on the response variables and mean effect sizes were calculated for each subgroup. The first subgroup was « experimental conditions » that included a comparison of controlled vs. field conditions and their combination. Controlled conditions

consist of experiments conducted in growth chambers, greenhouses, and tunnels. The second subgroup was « biological seed treatments » that comprised seed treatments with plant extracts (PE), plant derived products (PDP), or microorganisms (M). The latter included either bacteria or fungi as a subgroup. The third subgroup was « crop groups » which included cereals, horticultural, industrial, or leguminous crops. The fourth subgroup was « the target biotic stress » including plant pathogenic fungi, oomycetes, bacteria, nematodes, viruses, a pathogen complex, or no biotic stress conditions (i.e., negative control). The situation of pathogen complex includes more than one type of biotic stress that often occur under field conditions (Lamichhane and Venturi 2015; Rojas et al. 2016; van Agtmaal et al. 2017; You et al. 2020). The fifth subgroup was « climate zones » based on the zone of field studies considered in the meta-analysis, which were tropical, arid, temperate climate with no dry season (NDS), temperate climate with dry season (DS), or continental climate (C). The climate zones were determined using an online search of the location of the study on the website (<https://en.climate-data.org/>). The differences between subgrouped categories were considered significant if their confidence intervals did not overlap.

3 Results and discussion

3.1 Heterogeneity test

The Q test was significant for all response variables except for CY showing that a portion of the heterogeneity can be explained by subgrouping the studies into different categories. In contrast, the Q_v tests indicated that the heterogeneity of SG ($Q_v = 47.2$) and CY ($Q_v = 498.9$) was not significant (Table 1). Using the fixed-effects, I^2 statistic showed considerable heterogeneity for all response variables except for CY. When I^2 statistics were calculated as random-effect, the heterogeneity was not important for SG, DC, and CY while substantial heterogeneity was found for SE and PB (Table 1). Therefore, we used Q_v for further analysis to calculate \bar{R} . Subgrouping of the studies into different categories allowed us to reduce the heterogeneity of the data in some cases (Tables 2 and 3). For example, the heterogeneity of SE data was low and non-significant under tropical and arid climates (Table 2).

3.2 Overall effectiveness of biological seed treatments

Overall, when all study factors were combined, biological seed treatments significantly improved SG ($7 \pm 6\%$) and SE ($91 \pm 5\%$) compared with the untreated seeds (Fig. 2a). The gain in SE due to the planting of biologically treated seeds

Table 1 Heterogeneity among the effect sizes of studies. The heterogeneity was calculated by chi square (Q) and I^2 tests taking into account both fixed- and random-effects for the response variables. SG,seed germination; SE, seedling emergence; PB, plant biomass; DC, disease control; CY, crop yield. **significant at $p < 0.01$; ns, not significant.

Response variable	No. study	No. observation	Q		I^2	
			Fixed	Random	Fixed	Random
SG	64	754	4767.54**	47.21 ^{ns}	84.21	0
SE	126	2114	38343.67**	16226.15**	94.50	86.98
PB	153	1509	9040.04**	5449.26**	83.32	72.33
DC	210	2964	11887.13**	3301.37**	75.07	10.25
CY	163	1255	877.33 ^{ns}	498.99 ^{ns}	0	0

was much higher under controlled conditions ($123 \pm 8\%$) compared with that under field conditions ($56 \pm 6\%$). Likewise, biological seed treatments significantly improved PB (53

$\pm 5\%$) and DC ($55 \pm 1\%$) compared with the untreated seeds (Fig. 2a). Disease control efficacy due to biological seed treatments was significantly different both under controlled (59

Table 2 Heterogeneity among different study factors and response variables as calculated by random-effects chi square (Q_w) tests. SG, seed germination; SE, seedling emergence; PB, plant biomass; DC, disease control; CY, crop yield; df, degree of freedom; PDP, plantderived products; PE, plant extracts; M, microorganisms; –, no data were available for the analysis; NDS, temperate climate with no dry season; DS, temperate climate with dry season; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

Groups	SG		SE		PB		DC		CY	
	Df	Q_v	Df	Q_v	Df	Q_v	Df	Q_v	Df	Q_v
Experimental conditions										
Controlled	–	–	1021	11369.6**	–	–	1728	2358.1**	220	127.9 ^{ns}
Field	–	–	1091	5046.5**	–	–	1232	779.5 ^{ns}	1033	933.6 ^{ns}
Climate zones										
Tropical	–	–	26	26.3 ^{ns}	–	–	221	156.5 ^{ns}	101	101.5 ^{ns}
Arid	–	–	53	9.3 ^{ns}	–	–	338	303.2 ^{ns}	251	99.5 ^{ns}
Temperate NDS	–	–	26	630.2**	–	–	215	134.8 ^{ns}	238	223.7 ^{ns}
Temperate DS	–	–	45	94.4**	–	–	140	94.3 ^{ns}	135	214.8**
Continental	–	–	506	3325.0**	–	–	211	131.4 ^{ns}	254	220.9 ^{ns}
Crop groups										
Cereal	404	68.8 ^{ns}	441	797.1**	561	3779.9**	986	2065.6**	520	225.4 ^{ns}
Horticultural	348	31.7 ^{ns}	611	9956.9**	403	154.7 ^{ns}	917	507.9 ^{ns}	170	55.3 ^{ns}
Industrial	17	5.8 ^{ns}	297	2020.2**	182	227.5*	289	187.8 ^{ns}	135	51.87 ^{ns}
Leguminous	195	54.2 ^{ns}	758	3293.4**	357	472.4**	766	407.2 ^{ns}	425	429.6 ^{ns}
Biotic stresses										
Control	527	27.7 ^{ns}	361	81.4 ^{ns}	549	540.0 ^{ns}	118	88.7 ^{ns}	194	120.3 ^{ns}
Complex	7	0.1 ^{ns}	325	603.9**	66	90.0*	358	257.4 ^{ns}	194	201.6 ^{ns}
Fungi	195	41.7 ^{ns}	722	2474.4**	354	2633.6**	1647	2436.9**	394	415.4 ^{ns}
Bacteria	–	–	14	4.4 ^{ns}	19	26.6 ^{ns}	231	177.6 ^{ns}	–	–
Oomycetes	–	–	603	11963.5**	165	197.4*	309	296.1 ^{ns}	24	22.7 ^{ns}
Nematode	–	–	–	–	47	66.0*	93	97.1 ^{ns}	56	11.5 ^{ns}
Virus	–	–	–	–	–	–	73	75.0 ^{ns}	–	–
Seed treatments										
PDP	32	1.6 ^{ns}	90	201.7**	15	16.6 ^{ns}	111	528.5**	24	3.2 ^{ns}
PE	205	35.9 ^{ns}	173	186.1 ^{ns}	39	44.2 ^{ns}	134	65.7 ^{ns}	13	4.5 ^{ns}
M	514	36.3 ^{ns}	1848	15709.6**	1452	5349.4**	2714	1946.7 ^{ns}	1214	431.5 ^{ns}
Bacteria	380	92.2 ^{ns}	1012	8152.7**	1184	4955.5**	1806	1263.1 ^{ns}	932	841.6 ^{ns}
Fungi	128	14.1 ^{ns}	740	6222.0**	222	256.2 ^{ns}	795	561.6 ^{ns}	217	111.9 ^{ns}

Table 3 Heterogeneity among different study factors and response variables as calculated by random-effects chi square (Q_w) tests. SG, seed germination; SE, seedling emergence; PB, plant biomass; DC,disease control; CY, crop yield; df, degree of freedom; –, no data were available for the analysis; ** $p < 0.01$; * $p < 0.05$; ns, not significant.

Groups	SG		SE		PB		DC		CY	
	Df	Q_v	Df	Q_v	Df	Q_v	Df	Q_v	Df	Q_v
Key groups of bacteria										
<i>Azospirillum</i> spp.	19	0.9 ^{ns}	–	–	17	10.3 ^{ns}	–	–	19	0.8 ^{ns}
<i>Bacillus</i> spp.	105	7.2 ^{ns}	277	276.1 ^{ns}	286	491.2 ^{**}	380	189.9 ^{ns}	237	162.8 ^{ns}
<i>Burkholderia</i> spp.	–	–	89	649.1 ^{**}	106	111.5 ^{ns}	47	0.5 ^{ns}	17	19.5 ^{ns}
<i>Paenibacillus</i> spp.	–	–	17	23.8 ^{ns}	9	0.3 ^{ns}	–	–	9	11.1 ^{ns}
<i>Pseudomonas</i> spp.	151	68.3 ^{ns}	318	1720.5 ^{**}	503	504.0 ^{ns}	961	800.1 ^{ns}	446	445.1 ^{ns}
<i>Rhizobium</i> spp.	–	–	36	39.1 ^{ns}	8	10.0 ^{ns}	30	10.1 ^{ns}	26	13.9 ^{ns}
<i>Serratia</i> spp.	25	2.3 ^{ns}	–	–	10	11.1 ^{ns}	33	30.4 ^{ns}	14	10.3 ^{ns}
<i>Streptomyces</i> spp.	–	–	30	118.7 ^{**}	27	35.2 ^{ns}	39	37.4 ^{ns}	–	–
Key groups of fungi										
<i>Clonostachys</i> spp.	–	–	36	239.6 ^{**}	–	–	12	18.9 ^{ns}	–	–
<i>Gliocladium</i> spp.	–	–	73	421.7 ^{**}	–	–	78	84.8 ^{ns}	14	16.3 ^{ns}
<i>Penicillium</i> spp.	–	–	24	18.8 ^{ns}	22	28.6 ^{ns}	22	16.1 ^{ns}	6	1.4 ^{ns}
<i>Trichoderma</i> spp.	98	10.9 ^{ns}	567	5219.8 ^{**}	122	140.7 ^{ns}	474	293.8 ^{ns}	166	125.0 ^{ns}

$\pm 1\%$) and field ($48 \pm 2\%$) conditions. Biological seed treatments had significant impact on CY ($21 \pm 2\%$) compared with the untreated seeds (Fig. 2a). CY improvement due to biological seed treatments was much higher under controlled conditions ($18 \pm 6\%$) than that under field conditions ($6 \pm 2\%$). For all the five response variables, the improvement due to biological seed treatments was more pronounced under controlled conditions compared with that under field conditions (Fig. 3).

The planting of biologically treated seeds systematically provided higher benefits under controlled conditions than in the field. This is not surprising as the efficacy of any seed treatment is reduced under field conditions due to a myriad of abiotic and biotic factors that interact under these conditions (Lamichhane et al. 2018, 2020a). However, our meta-analysis clearly shows that the planting of biologically treated seeds has a huge potential to enhance yield gain and to increase profitability even under field conditions due to improved disease control.

Compared with other variables, SE benefitted the most due to the planting of biologically treated seeds. This improved SE was mainly due to an enhanced level of control of diseases caused by soil-borne pathogenic fungi and oomycetes (Rojas et al. 2016; Foster et al. 2017; Serrano and Robertson 2018). While biological seed treatments enhanced SE via better control of individual plant pathogenic oomycetes and fungi, SE was improved to a lower extent in situations characterized by the pathogen complex. This means that, biological seed treatments are effective in controlling individual pathogens, but less effective against a disease complex involving different pathogens as shown previously (You et al. 2020).

3.3 Biological seed treatment types

Among different products used for biological seed treatments, seeds treated with M significantly improved SG ($9 \pm 7\%$) compared with other products (Fig. 2b). No significant effect of seeds treated with fungal microorganisms was found on SG ($p = 0.05$) while biological seed treatments with beneficial bacteria significantly enhanced SG ($7 \pm 4\%$). Both PDP and PE slightly improved SG but without any significant difference compared with other biological seed treatments (Fig. 2b).

Among the response variables, SE had the highest response ratios due to biological seed treatments (Fig. 3). Seed treatment with M was the most effective in improving SE ($102 \pm 6\%$) compared with those with PE ($7 \pm 6\%$) and PDP ($21 \pm 15\%$; Fig. 2b). Both bacterial and fungal microorganisms used for seed treatments improved SE compared with untreated seeds, with fungal microorganisms being more effective ($133 \pm 13\%$) than their bacterial counterparts ($85 \pm 6\%$).

Significant increase in PB was found with seed treated with PE ($37 \pm 13\%$) and M ($54 \pm 6\%$) while seed treated with PDP did not have any significant impact on PB ($13 \pm 23\%$) (Fig. 2b). Both bacterial and fungal microorganisms used for biological seed treatments significantly improved ($p < 0.05$) PB by 56% and 38%, respectively.

All sub-grouped products used for biological seed treatments significantly provided ($p < 0.05$) a more effective DC with significant difference in their effectiveness (Fig. 2b). The magnitude of DC obtained was similar between seed treated with M ($52 \pm 1\%$) and PE ($53 \pm 7\%$) while DC was significantly higher with seeds that were treated with PDP ($75 \pm 3\%$). Biological seed treatments with beneficial fungi or

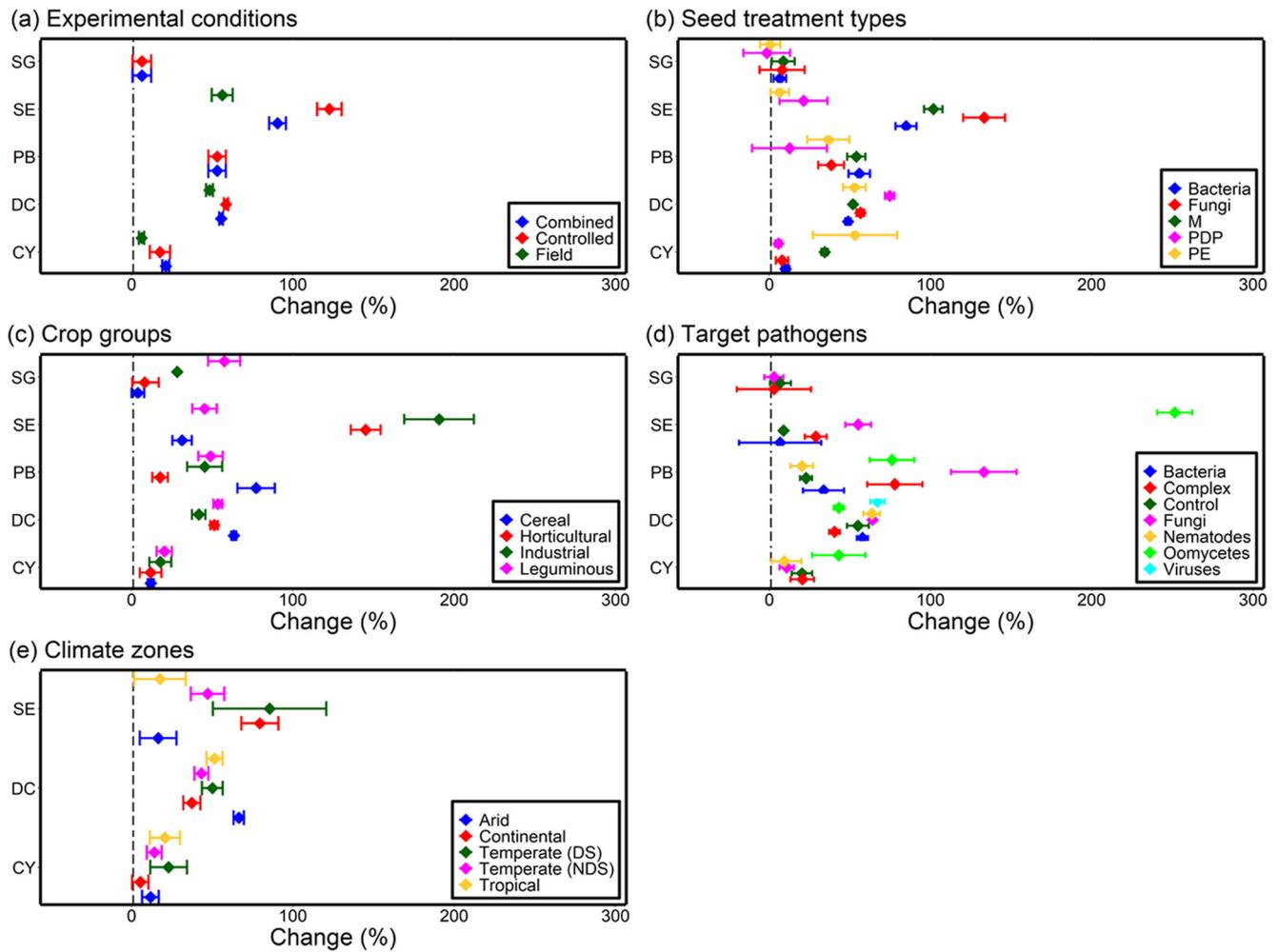


Fig. 2 Changes (%) in response variables due to biological seed treatments compared with untreated seeds (i.e., control; see Eq. 8 for detailed information). The changes are grouped by experimental conditions (a), seed treatment types (b), crop groups (c), target pathogens (d), and climate zones (e). Error bars show 95% confidence intervals (CI). No overlap of error bars with zero indicates that biological treatments significantly affected the response variables. Differences among sub-group categories are not significant when error bars are

bacteria provided DC to a similar extent (fungi +57% vs. bacteria +49%) while their effectiveness was significantly different ($p < 0.05$) compared with untreated seeds (Fig. 2b).

Commonly used microorganisms (bacteria and fungi) for seed treatments and their response values are listed in Table S1. Likewise, the most effective bacteria and fungi in improving crop performance and yield, when applied with seed treatments, are reported in Fig. 4 a and b, respectively. All response variables but SG were significantly improved when bacteria or fungi were used for seed treatments.

Among bacteria (Fig. 4a), seed treatments with *Burkholderia* spp. were the most effective in terms of improved SE ($180 \pm 38\%$) followed by those with *Paenibacillus* spp. ($115 \pm 63\%$), *Pseudomonas* spp. ($82 \pm 13\%$), *Rhizobium* spp. ($59 \pm 20\%$), and *Bacillus* spp. ($10 \pm 4\%$). No significant change in

overlapped. No error bars indicate that the symbol is larger than the error. SG, seed germination; SE, seedling emergence; PB, plant biomass; DC, disease control; CY, crop yield; PDP, plant derived products; PE, plant extracts; M, microorganisms; NDS, temperate climate with no dry season; DS, temperate climate with dry season. The number of studies and observations for each response variable is reported in Table 1.

PB was observed when seeds were treated with *Azospirillum* spp. while *Rhizobium* spp. ($66 \pm 57\%$) followed by *Streptomyces* spp. ($53 \pm 35\%$), *Bacillus* spp. ($36 \pm 8\%$), *Pseudomonas* spp. ($27 \pm 4\%$), *Paenibacillus* spp. ($21 \pm 16\%$), *Burkholderia* spp. ($19 \pm 7\%$), and *Serratia* spp. ($18 \pm 13\%$) seed treatments significantly enhanced PB, in decreasing order of importance. All but *Burkholderia* spp. provided significant DC with *Serratia* spp. ($68 \pm 7\%$) being the most effective, followed by *Streptomyces* spp. ($51 \pm 9\%$), *Bacillus* spp. ($49 \pm 4\%$), *Pseudomonas* spp. ($48 \pm 2\%$), and *Rhizobium* spp. ($32 \pm 12\%$). Significant effect on CY was observed when seeds were treated with *Bacillus* spp. ($15 \pm 5\%$), *Rhizobium* spp. ($13 \pm 6\%$), and *Pseudomonas* spp. ($8 \pm 3\%$), in decreasing order of effectiveness.

As for fungi (Fig. 4b), SE was significantly improved when seed treatments were performed with *Gliocladium* spp. (234

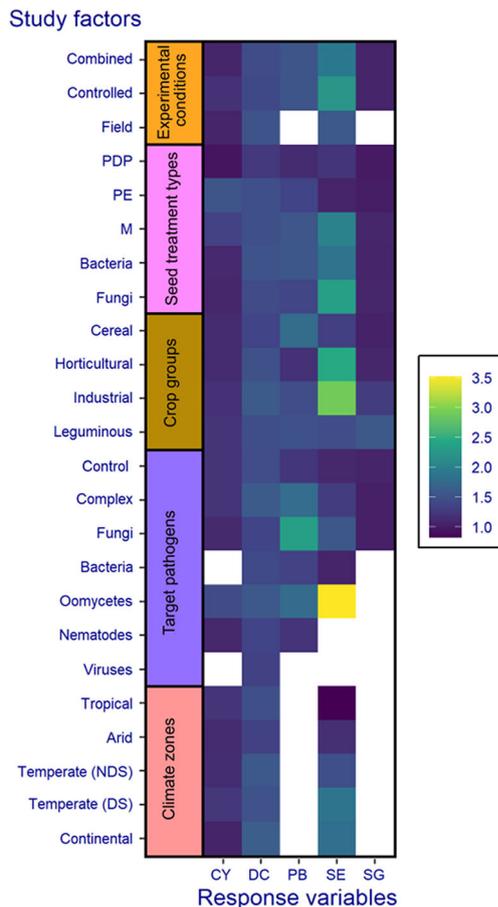


Fig. 3 Weighted average of the response ratio of the measured/studied variables for different study factors as shown by heat map graph (see Eq. 5 for detailed information). The weighted average is grouped by experimental conditions (a), seed treatment types (b), crop groups (c), target pathogens (d), and climate zones (e). The weighted average of the response ratio >1 in the heat map indicates a positive response while a value of <1 shows a negative response. The blank part in the heat map graph was due to no data availability. SG, seed germination; SE, seedling emergence; PB, plant biomass; DC, disease control; CY, crop yield; PDP, plant derived products; PE, plant extracts; M, microorganisms; NDS, temperate climate with no dry season; DS, temperate climate with dry season. The number of studies and observations for each response variable is reported in Table 1.

$\pm 52\%$), followed by *Penicillium* spp. ($179 \pm 29\%$), *Clonostachys* spp. ($168 \pm 68\%$), and *Trichoderma* spp. ($141 \pm 16\%$). All but *Clonostachys* spp. and *Gliocladium* spp. seed treatments significantly increased PB with *Penicillium* spp. being the most effective ($70 \pm 34\%$) compared with *Trichoderma* spp. ($31 \pm 11\%$). In contrast, seed treatments with all four fungal groups significantly enhanced DC with *Clonostachys* spp. being the most effective ($69 \pm 15\%$) followed by *Gliocladium* spp. ($59 \pm 5\%$), *Trichoderma* spp. ($57 \pm 3\%$), and *Penicillium* spp. ($53 \pm 13\%$). Finally, only seed treatments with *Trichoderma* spp. significantly enhanced CY ($31 \pm 6\%$).

Biological seed treatments with PE provided the most significant CY increase ($53 \pm 26\%$) followed by those with M ($34 \pm 2\%$). In contrast, biological seed treatments with PDP

negatively affected CY (-6%) compared with untreated seeds (Fig. 2b). Both bacterial and fungal microorganisms used for biological seed treatments significantly improved CY compared with untreated seeds (fungi $+8\%$; $p < 0.05$ vs. bacteria $+10\%$; $p < 0.05$). More details about PDP and PE treatments can be found in Table S2 and Supplementary Data 3. Only response ratio values are reported for these treatments due to a large variation between PDP and PE treatments that did not allow us to analyze these data.

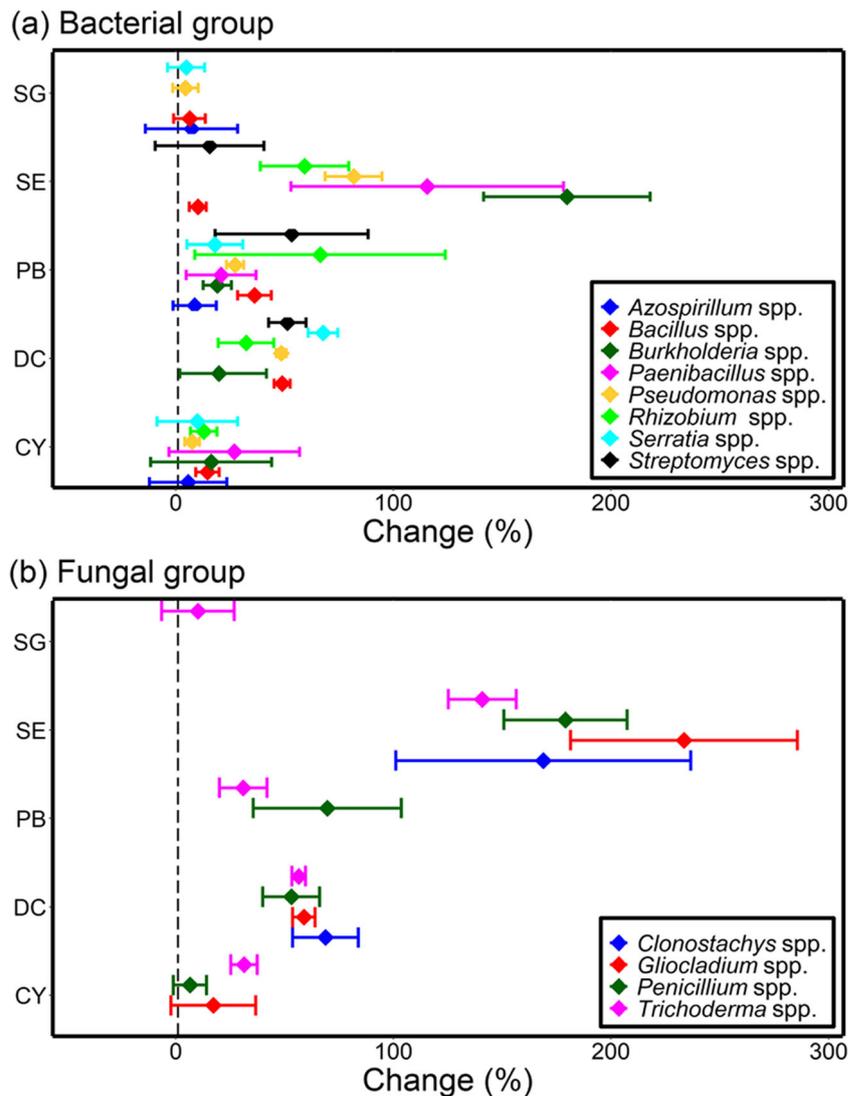
Application of beneficial microorganisms to seeds allows the placement of microbial inocula into soil, thereby facilitating a rapid colonization of seedling roots and offering protection against soil-borne pests and pathogens (Papavizas 1985; Couillerot et al. 2009; O’Callaghan 2016). At the same time, replacing chemical seed treatments with biological seed treatments helps to ensure natural functioning of seed-associated bacteria, which represent an important reservoir of microorganisms playing an essential role for early plant development and vigor (Matsumoto et al. 2021). Avoiding the planting of chemically treated seeds also means enhancing seed and plant endophytes that have important functions in their host including disease suppression (Haridoim et al. 2015; Berg et al. 2016). These endophytes are negatively impacted by chemical seed treatments (Vasanthakumari et al. 2019; Chen et al. 2020).

3.4 Crop groups

SG enhancement due to biological seed treatments was significantly different among the crop groups (Figs. 2c and Fig. 3). Biological seed treatments significantly improved SG of leguminous ($58 \pm 10\%$) and industrial crops ($28 \pm 0\%$) while no significant improvement in SG was observed for cereal ($p = 0.05$) and horticultural ($p = 0.05$) crops (Fig. 2c). Biological seed treatments had the lowest effect on SE improvement in cereal ($31 \pm 6\%$) while it provided the highest benefit for industrial ($191 \pm 22\%$) and horticultural crops ($145 \pm 9\%$). This can be explained by the fact that cereals are the most vulnerable crop groups as they are most often attacked by a myriad of seed- and soil-borne pathogens (Majumder et al. 2013) across all phases of the crop cycle.

In all crop groups, biological seed treatments significantly increased ($p < 0.05$) PB compared with untreated seeds. Statistically significant differences were observed among crop groups in terms of increase in PB due to biological seed treatments with cereals drawing the most important gain ($77 \pm 12\%$) followed by leguminous ($49 \pm 8\%$), industrial ($45 \pm 11\%$), and horticultural crops ($18 \pm 5\%$). The gain in PB of cereal crops due to biological seed treatments was significantly different ($p < 0.05$) compared with that of the other crop groups (Fig. 2c). In contrast, no significant difference ($p = 0.05$) in PB increase due to biological seed treatments was observed between industrial and leguminous crops although both of them

Fig. 4 Major types of microorganisms used for seed treatments. These microorganisms include groups of bacteria (a) and fungi (b) that improve crop performance and yield when applied with seed treatments. SG, seed germination; SE, seedling emergence; PB, plant biomass; DC, disease control; CY, crop yield. The number of studies and observations for each response variable is reported in Table 1.



had a significant PB gain ($p < 0.05$) compared with that of horticultural crops.

Disease control due to biological seed treatments was observed among all crop groups with cereals benefiting the most ($63 \pm 2\%$) followed by leguminous ($54 \pm 3\%$), horticultural ($51 \pm 2\%$), and industrial crops ($42 \pm 4\%$). Significant differences in DC ($p < 0.05$) in cereals crops were observed compared with leguminous, horticultural, and industrial crops. In contrast, no significant difference ($p = 0.05$) in DC due to biological seed treatments was observed among leguminous and horticultural crops (Fig. 2c).

A significant effect of biological seed treatments on CY was observed for all crop groups with leguminous crops taking the most important advantage ($20 \pm 5\%$), followed by industrial ($18 \pm 7\%$), cereal ($12 \pm 2\%$), and horticultural ($12 \pm 7\%$) crops. There was no significant difference ($p = 0.05$) between crop groups in terms of CY improvement due to biological seed treatments, except for the difference between cereals and

legumes, with the latter taking significantly higher CY benefits than the former ($p < 0.05$).

3.5 Biotic stresses

No significant improvement ($p = 0.05$) on SG due to biological seed treatments was found (Fig. 2d). In contrast, biological seed treatments significantly improved SE via a better DC due to plant pathogenic oomycetes ($252 \pm 11\%$), followed by fungi ($55 \pm 8\%$), the pathogen complex ($29 \pm 7\%$), and even under no pathogen inoculation conditions ($9 \pm 2\%$). SE due to biological seed treatments was not significantly increased when diseases were caused by bacterial pathogens (7% ; $p = 0.05$). Biological seed treatments significantly increased ($p < 0.05$) PB either under biotic stresses or under control conditions compared with untreated seeds (Fig. 2d). Biological seed treatments increased PB through significantly better control of diseases caused by plant pathogenic fungi

(133±20%), followed by the pathogen complex (78±17%), oomycetes (76±14%), bacteria (34±13%), and nematode pathogens (20±7%).

Biological seed treatments were the most effective in reducing seed and seedling diseases caused by plant pathogenic viruses (67±4%) followed by those caused by fungi (64±1%), nematodes (64±5%), bacteria (57±3%), oomycetes (43±3%), and the pathogen complex (41±3%). Significant differences ($p<0.05$) in DC were observed among diseases caused by plant pathogenic viruses, fungi, and nematodes compared with those caused by other biotic stresses or under no inoculation conditions (Fig. 2d).

Biological seed treatments improved CY through significantly better control of plant pathogenic oomycetes (43±17%), the pathogen complex (21±7%), and pathogenic fungi (11±4%). In contrast, no significant yield gain response ($p=0.05$) due to biological seed treatments was observed due to better control of plant pathogenic nematodes (Fig. 2d). Likewise, no significant CY increase due to biological seed treatments ($p=0.05$) was observed between the pathogen complex and control conditions or between stress due to pathogenic fungi and nematodes. No CY data were available for stress caused by plant pathogenic bacteria and viruses (Fig. 3).

3.6 Climate zones

Biological seed treatments significantly enhanced ($p<0.05$) SE across all but tropical climate zones. The magnitude of SE increment was significantly higher in temperate DS (86±35.16%), followed by continental (80±12%), and temperate NDS (47±10%) climate zones, compared with the arid zone (17±11%) (Fig. 2e). Among the response variables, SE due to biological seed treatments had the most important gain compared with DC and CY (Fig. 3). Significant negative reduction in SE due to biological seed treatments was observed under tropical climate (18±16%). DC under field conditions due to biological seed treatments was significantly increased in arid (67±3%), followed by tropical (52±5%), temperate DS (50±6%), temperate NDS (43±4%), and continental (37±5%) climate zones (Figs. 2e and 3).

Biological seed treatments significantly increased CY gain that was the highest under temperate DS (23±11%) followed by tropical (21±9%), temperate NDS (14±5%), arid (12±5%), and continental (6±5%) climate zones. There was no significant difference ($p=0.05$) between climate zones in terms of CY improvement due to biological seed treatments, except for the difference between continental climate zone and temperate DS or tropical climate zones.

We found a significant effect of climate on the effectiveness of biological seed treatments in improving crop development and yield due to enhanced disease control. For instance, SE was negatively affected by biological seed treatments under tropical climate zones compared with others, which could

be due to the effect of soil moisture, elevated temperature, or their interactions. Indeed, regions with a lower frequency of rainfall are more likely to benefit from the planting of biologically treated seeds, as observed for seed priming (Carrillo-Reche et al. 2018).

The planting of biologically treated seeds significantly increased CY gain across all climate zones compared with the untreated seeds. However, the extent of benefit provided by this practice was different among the climate zones with all but continental climate zones benefitting the least. Our results corroborate the conclusion of a recent meta-analysis where on-farm seed priming had the largest positive response on CY under arid or semi-arid climates (Carrillo-Reche et al. 2018). We found that biological seed treatments did not improve SE in tropical regions but enhanced DC in the same regions. This implies that CY improvement in this region was mainly due to an increased DC after SE. However, in other climate zones, improved CY was related both to enhanced SE and increased DC due to the planting of biologically treated seeds.

4 Conclusion

Information on the potential of different biological seed treatments across different crop groups or climatic zones, in terms of crop performance, is particularly useful for stakeholders of the agri-food system for decision making. Based on our results, the planting of biologically treated seeds should be encouraged across climate zones or crop groups where this practice already ensures increased crop performance. In contrast, further improvements of the currently used biological seed treatment methods, and the development of new ones, should be considered for areas or crop groups that provide lower yield gain.

The planting of biologically treated seeds with microorganisms can also mitigate the impact of climate change due to improved tolerance to abiotic stresses such as heat stress (Abd El-Daim et al. 2014; O'Callaghan 2016). Indeed, no inoculation conditions considered in this meta-analysis were related to treatments without artificial inoculation of plant pathogens although other abiotic stresses were naturally occurring under these conditions. Significant improvement in SE and CY under non-inoculated conditions observed in this meta-analysis is a clear indication that biological seed treatments have potential to increase crop performance and yield under climate change.

Finally, our meta-analysis showed that biological seed treatments have potential to ensure long-term sustainability of the agri-food system with no or reduced human health and environmental impacts. Our results therefore are of great significance for the stakeholders who are looking to foster the sustainability of the agri-food system.

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Code availability Not applicable.

Authors' contributions Conceptualization: JRL; Methodology: ES, JRL, DCC; Investigation: ES, JRL; Visualization: JRL, ES, DCC; Writing original draft: JRL; Writing, review & editing: ES, JRL.

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Data availability All the data used to write this bibliographic review come from the publications listed in the supplementary materials.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

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