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Biocontrol of clubroot disease: how successful are endophytic fungi and bacteria?

Susann Auer · Jutta Ludwig-Müller

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Abstract The commercial aspect of growing Brassica crops has always been influenced by the worldwide occurrence of the clubroot pathogen, *Plasmodiophora brassicae*. Clubroot symptoms reduce crop yield dramatically and the resilient protist is hard to eradicate from infested soils. Chemical treatments are not so efficient and their use is allowed only in a few areas of the world, none of them in the EU. The majority of clubroot control is mediated by using resistant crops, but not all species have good or durable resistance sources available, and these can be overcome by evolving or new *Plasmodiophora* pathotypes. Some commercially available biocontrol agents have been tested and found to reduce clubroot on crops such as rapeseed, cauliflower and Chinese cabbage to some extent. More biocontrol organisms have been isolated and described in recent decades but for many commercial application is still a long way off. In this review we summarize trends for bacterial and fungal endophytes for clubroot biocontrol as well as mechanisms behind the effects reported, such as antibiosis, defense induction or competition for space and nutrients. There are indeed plenty of studies on biocontrol of clubroot but not many have reached a point where the biocontrol agents are ready to be applied at field scale. The potential of endophytic microbes in pest management against clubroot disease is huge.

Keywords Biocontrol · Brassica crops · Clubroot · Endophyte · *Plasmodiophora brassicae* · Protist

S. Auer · J. Ludwig-Müller (✉)
Faculty of Biology, Technische Universität Dresden, 01062 Dresden, Germany
e-mail: Jutta.Ludwig-Mueller@tu-dresden.de

Introduction

Clubroot disease was first reported in the USA in the year 1852 (cf. Hirai, 2006; Karling, 1968) and the causal agent was identified in 1878 by Woronin (Woronin, 1878). Not much later the disease was also reported for the first time in Japan (cf. Hirai, 2006). Clubroot has now been identified in many countries around the world as one of the largest economic problems in Brassica crop cultivation (Botero et al., 2019; Gossen et al., 2015; Ren et al., 2016; Zamani-Noor et al., 2022). Clubroot-infected plants show large root galls (=clubs) which ultimately turn the roots into a strong metabolic sink of carbohydrates and other nutrients from the leaf tissues (Keen & Williams, 1969; Malinowski et al., 2019). This leads to a dramatic reduction of green plant biomass compared to healthy plants and causes large yield losses in Brassica cultivars (Dixon, 2014).

The clubroot pathogen *Plasmodiophora brassicae* is an aggressive unicellular protist with a complex life cycle that makes management of the disease with agrochemicals a challenge. The disease cycle starts with durable resting spores of *P. brassicae* left over from previously decayed plant root galls that can stay dormant in contaminated soils for decades until presented with a suitable host. All weeds from the Brassicaceae can be infected as well as crop plants such as rapeseed / canola, swede (*Brassica napus*), other crops from *B. rapa* and *B. oleracea* species like kale, turnip, white and red cabbage, broccoli, cauliflower, and oil radish (*Raphanus sativus*) (Dixon, 2009). During the primary infection,

emerging zoospores of *P. brassicae* infect fresh root hairs and form primary plasmodia in root hairs and epidermal cells within 7 days of the initial zoospore contact (Liu et al., 2020). The plasmodia in these root hairs then develop into mature zoosporangia which ultimately release secondary zoospores into the lumen of epidermal root cells (Liu et al., 2020). After this, secondary plasmodia develop in the inner root cortex tissue and produce large amounts of resting spores in the cortical cells. The secondary infection is characterized by the typical swelling of root tissue that can easily be observed as a trademark symptom of the clubroot disease.

Chemical control of clubroot disease is challenging due to the biotrophic nature of the pathogen and the durable resting spore deposits in agricultural soil. Clubroot-reducing fungicides such as carbendazim, cyazofamid and fluazinam are banned in the European Union which leaves sustainable crop management practices with resistant cultivars and biocontrol approaches as the only options here (Donald & Porter, 2009; Liao et al., 2022; Peng et al., 2011; Struck et al., 2022). Sustainable crop management includes the maintenance of a healthy soil structure, fertilizer input only as needed and measures that ensure good soil health and great microbial diversity (Zhang et al., 2019).

However, what is biological control? The definition encompasses using living organisms to control plant pathogens or pests, so called biocontrol agents, (Stenberg et al., 2021), and is different from plant strengtheners or biostimulants such as seaweed extracts that have been tested against clubroot as well (Kammerich et al., 2014; Wite et al., 2015). One challenge for cost efficient crop production is that the most sustainable methods are often not the cheapest ones on the market (Parnell et al., 2016). In order to meet the EU goals of a 50% reduction of chemical pesticide use and prioritization of integrated pest management as well as preventing disease resistance, a strong focus on sustainable crop management methods including biocontrol is needed (Sustainable Use of Pesticides Directive 2009/128/EC; https://eur-lex.europa.eu/eli/dir/2009/128/oj). Since chemical, genetic, or biological methods have different targets during the life cycle of a pathogen, control approaches should be combined to achieve better effects (Ludwig-Müller, 2016; Peng et al., 2011; Struck et al., 2022). For example, disease resistant crops should be used together with other options to control clubroot, and biological control is an option.

Strategies for the control and biocontrol of clubroot disease have been reviewed recently (Ahmed et al., 2020; Struck et al., 2022). Struck et al. (2022) provide a good overview of agricultural practices useful for sustainable clubroot management. What is missing so far is an overview of bacterial and fungal biocontrol agents and the specific mode of action of biocontrol microbes against clubroot which we aim to provide here. In this review we focus on the biocontrol of clubroot by endophytic organisms. Endophytes are microbes that live asymptomatically in plant tissues and form a symbiotic relationship with their host (Fesel & Zuccaro, 2016; Ludwig-Müller, 2015; White et al., 2019). Endophytic microorganisms are well suited for biocontrol since they spend a considerable part of their life cycle within living plant tissue and are therefore well adapted to their host (Latz et al., 2018). The majority of land plants are inhabited by endophytic bacteria and fungi (Khare et al., 2018) and they fulfill important functions for their host plant. Endophytes enhance nutrient availability and adaption to environments (Das & Varma, 2009), increase the defense and stress tolerance of their host (Bulgarelli et al., 2013; Busby et al., 2016) and influence plant development (Khare et al., 2018).

Endophytes play an increasingly important role as biocontrol agents (BCAs) of plant diseases and are especially helpful against soil-borne pathogens that are hard to control, such as the clubroot pathogen *P. brassicae*. Brassica species produce strong antimicrobial compounds, the glucosinolates, which might prevent them from forming beneficial mycorrhizal interactions (Glenn et al., 1988; Vierheilig et al., 2000). Brassicas therefore benefit more from endophytic interactions with bacteria and fungi (Poveda et al., 2022).

Approaches with endophytes used as biocontrol against clubroot disease

For this review, we surveyed the peer-reviewed literature for biocontrol microorganisms used against clubroot disease. Our search in November 2022 included the words “biocontrol” and “Plasmodiophora” or “clubroot”/”club root” in various combinations in Web of Science and Google Scholar. Unfortunately,

a few manuscripts were not accessible to us either because of restrictions regarding the subscription of our institution or due to language barriers for research in languages other than English and German.

Our literature search revealed a total of eight fungal and 18 bacterial species with several strains exhibiting a potential for clubroot control (Table 1). Combinations of microbial strains as mixtures for biocontrol were also included, and at least eight combinations were tested. An experimental setup close to conditions in the field is preferable to study the effectiveness of BCAs against clubroot disease since Brassicas are cultivated in fields. However, this kind of setup is not accessible to all researchers and many plant pathologists study plant pathogen interactions in a controlled environment like climate chambers and greenhouses. The research we screened showed that the majority of experiments were carried out in greenhouses (46% which represents 35 of the 76 reported experiments), followed by field trials (29% with 22 experiments) and climate chambers (25% with 19 experiments). Of all these studies, 10 used two different growth conditions for the host plant, and one study used all three approaches.

The majority of reports were from Asian countries (57%), among them China (31%), Japan (10%), Korea (5%), Indonesia (5%), Philippines (5%) and Nepal (2%), followed by North America with Canada (17%), Europe (14%) with Germany (7%), Estonia, Denmark and Poland (each 2%) and South America (5%) with Brazil (2%) and Colombia (2%) and Australia with New Zealand (5%). The main inoculum sources for *P. brassicae* were field isolates from naturally infested soil from the area in which the studies were conducted, and in five studies the predominant pathotype occurring in that area was reported (15 reported sources, 35% of total reports). For 13 experiments the inoculum source was not reported or not specified, e.g. "root galls of Chinese cabbage" (30%), for 10 studies infested field soil was used (23%) and five studies (12%) used single spore isolates of *P. brassicae*.

Many studies lacked a detailed description of the BCA used. Six research groups used commercially available biopesticides (Botero et al., 2015; Gossen et al., 2016; Kurowski et al., 2009; Lahlali & Peng, 2014; Lahlali et al., 2011, 2013; Peng et al., 2011; Santos et al., 2017). In total an estimated amount of at least 30 different (labeled) strains were used as BCAs against clubroot in the studies in Table 1.

Is biocontrol effective against clubroot?

Sustainable clubroot management involves a combination of resistant cultivars combined with field sanitation measures to prevent further spread of clubroot resting spores, crop rotation, appropriate soil nutrition and the use of biocontrol options (Peng et al., 2011; Struck et al., 2022; Yu et al., 2015).

Figure 1 gives an overview of the relative biocontrol effect on the Disease Index (DI) of clubroot after application of fungal, bacterial and mixed microbial BCAs. The relative biocontrol effect is the efficacy of the applied microbes to reduce symptoms in clubroot-infected plants. The majority of studies reported a reduction of clubroot symptoms after BCA treatment, and the overall efficacy ranged from -28% (more severe symptoms observed with the BCA treatment) up to 100% (no clubroot symptoms after BCA treatment). These data present only a fraction of what was researched in that area due to the lack of detailed reporting of findings in the peer-reviewed studies considered for this paper and a publication bias towards only positive results in general. Many reports on the biocontrol of clubroot contain graphs to display the DI but not all of them include the data used to generate these figures or the calculated control effects for the DI. The lack of detailed reporting prevents the correct assessment of the biocontrol effect on the disease extent against clubroot and hinders replication efforts, a known problem in phytopathology literature already pointed out in other analyses (Ngugi et al., 2011; Sparks et al., 2023). Several data points in Fig. 1 originate from only a few studies and some studies investigated a low number of plants per treatment ($n < 10$) so the reliability of these results is hard to estimate (see Supplement 1 for the data used to create Fig. 1).

The overall trend seen in Fig. 1 is very promising though, as it seems that the use of BCAs against clubroot is a successful approach. It becomes clear as well, that a more thorough research database for specific species such as *Heteroconium* (*Cladophialophora*) *chaetospira* helps to assess the potential profitability of using a BCA. It also shows that commercially available biopesticides have a similar efficacy against clubroot as strains isolated from the local rhizosphere of clubroot-infested fields. In summary, the overview of biocontrol efficacy shows that there is still a lot of potential for new BCAs against clubroot. To be marketable, the

Table 1 Summary of endophytic biocontrol organisms (BCA) that have been used against clubroot disease in different hosts and cultivation environments. An x indicates that experiments were done in these experimental setups, 0 indicates that no experiments were done in these experimental setups. Plant hosts in this table are indicated as they are described in the original literature source

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Fungi								
Acremonium alternatum	*Acremonium alternatum* strain MUCL No. 12012 of the culture collection at the Mycotheque de L'Universite Catholique de Louvain, Belgium	single spore isolate e3 (Fähling et al., 2003)	*Arabidopsis thaliana* Col-0, *Brassica rapa* ssp. *pekinensis* cv. Granaat	x	x	0	Doan et al., 2010	Germany
Acremonium alternatum	Strain MUCL No. 12012	single spore isolate eH (Fähling et al., 2003)	*Arabidopsis thaliana*	x	0	0	Jäschke et al., 2010	Germany
Acremonium alternatum	Strain MUCL No. 12012	single spore isolate e3 (Fähling et al., 2003)	*B. napus* cv. Ability, Visby	0	x	0	Auer & Ludwig-Müller, 2014	Germany
Clonostachys rosea syn. Gliocladium catenulatum	biofungicide Prestop® (wettable powder; Verdera Oy) containing *Clonostachys rosea* isolate J1446, Prestop® product filtrate, fungal conidia suspension	field isolate from Alberta, Canada: predominantly pathotype 3	*B. napus* cv. Fortune RR	x	0	0	Lahlali & Peng, 2014	Canada
Clonostachys rosea	Prestop® wettable powder	field isolates: pathotypes 3 and 6 (Williams differential set) from Alberta and Muck Crops Research Station, Canada	*B. napus* cv. 46A76; Pioneer Hi-Bred, Shanghai pak choy *B. rapa* ssp. *chinensis* cv. Mei Qing Choi; Stokes Seeds Ltd	x	0	0	Gossen et al., 2016	Canada
Clonostachys rosea	isolate IK726 (isolated from barley roots) used as seed coating	*B. napus* galls from Køge, Denmark	*B. napus* cv. DK Exclaim, resistant *B. napus* cv. DK Platinum; Dekalb	x	0	0	Andersen et al., 2018	Denmark
Clonostachys rosea	Prestop® wettable powder	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	x	Peng et al., 2011	Canada
Heteroconium chaetospira curr. name *Cladophialophora chaetospira*	rhizosphere isolates from wheat fields: *Heteroconium chaetospira* isolates M4006 and H4007 (Japan)	field isolate of Chinese cabbage galls from Chiyokawa, Ibaraki, Japan	Chinese cabbage *B. campestris* cv. Muso	0	x	0	Narisawa et al., 1998	Japan

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Cladophialophora chaetospira	isolate H4007	field isolates from Iwama, Ibaraki, Japan, collected in 2001	Chinese cabbage *B. campestris* cv. Shin-Riso	0	0	x	Narisawa et al., 2000	Japan
Cladophialophora chaetospira	isolate MAFF238955	field isolates from Chiyokawa and Yachiyo, Ibaraki, Japan	Chinese cabbage *B. campestris* cv. Shin-Riso	0	x	x	Narisawa et al., 2005	Japan
Cladophialophora chaetospira	isolate BC2HB1 from Canadian forest soil from Narisawa et al. (2007)	not reported	*B. napus* cv. Fortune RR	x	0	0	Lahlali et al., 2014	Canada
Gliocladium virens (now*Trichoderma)*	SoilGard 12G® granules	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	0	0	Peng et al., 2011	Canada
Phoma glomerata	strain JCM9944	field isolate: root galls (*B. rapa* from Komoro, Nagano and Tochigi, Japan)	*B. rapa* cv. Ohsho, *B. campestris* var. Rapa Tokinashi-kokabu, Komatsuna, Nozawana; *B. oleraceae*	0	x	0	Arie et al., 1998	Japan
Phoma wasabiae	strain RI19	field isolate: root galls (*B. rapa* from Komoro, Nagano and Tochigi, Japan)	*B. rapa* cv. Ohsho, *B. campestris* var. Rapa Tokinashi-kokabu, Komatsuna, Nozawana; *B. oleraceae*	0	x	0	Arie et al., 1998	Japan
Trichoderma spp.	25 field isolates from infested soil near symptomless plants from Levin, New Zealand	infested field soil from Levin, NZ; macerated galls	*B. chinensis* cv. Wong-Bok	0	x	x	Cheah & Page, 1997	New Zealand
Trichoderma spp.	15 field isolates from infested soil near symptomless plants from Levin, New Zealand; in field trial isolates TC32, TC45 and TC63		*B. chinensis* cv. Wong-Bok, *B. oleraceae* cv. *botrytis* All Year Round	0	x	x	Cheah et al., 2000	New Zealand
Trichoderma spp.	Trichoderma inoculant T1	infested field soil from Banooy, Buguias, Benguet, Philippines	*B. oleracea capitata*, *B. rapa pekinensis*	0	0	x	Cuevas et al., 2011	Philippines

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Trichoderma spp.	indigenous garden soil isolates, e.g. *T. hamatum*, *T. harzianum*	infested garden soil from vegetable farmers in Bedugul, Bali, Indonesia	*B. oleracea* var. Capitata	0	x	0	Suada, 2017	Indonesia
Trichoderma spp.	local isolate Trichoderma KA	infested field soil	cabbage var. Scorpio	0	0	x	Bulcio & Nagpala, 2014	Philippines
Trichoderma spp.	isolates T22, TS and T69	infested field soil	cauliflower var. Rami	0	0	x	Timila, 2011	Nepal
Trichoderma harzianum	isolate T4, East China Unversity of Science and Technology	clubs from Chinese cabbage	Chinese cabbage	0	x	0	Yu et al., 2015	China
Trichoderma harzianum	Root Shield®, wettable powder, BioWorks Inc., USA	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	0	Peng et al., 2011	Canada
Trichoderma harzianum	*T. harzianum*-based biofungicide; ESALQ 1306 strain; emulsifiable concentrate	infested field soil from Nova Friburgo, Rio de Janeiro, Brazil	Cauliflower *B. oleracea var. botrytis* cv. Barcelona	0	x	x	Santos et al., 2017	Brazil
Serendipita indica syn. Piriformospora indica	seed treatment with powder inoculum of *S. indica*	not reported	*B. napus* ACS N39	x	0	0	Sedaghatkish et al., 2021	Canada
Bacteria								
Actinomycetes sp.	strains isolated from Chinese cabbage cv. Sam-Bok from various locations, Korea	not reported	Chinese cabbage	0	x	0	Lee et al., 2008	Korea
Alcaligenes faecalis	Juj3 strain isolated from rhizosphere of healthy cabbage in Baoji, Shaanxi, China	field isolate from infected Chinese cabbage	cabbage cv. Haoyuan, Chinese cabbage cv. Qingza No. 3	0	x	x	Jia et al., 2022	China
Bacillus amyloliquefaciens	Taegro® wettable powder	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	0	Peng et al., 2011	Canada
Bacillus amyloliquefaciens	rhizosphere isolates from asymptomatic rapeseed roots on clubroot infested fields in Dangyang county, Hubei, China	field isolates from infected rapeseed clubs	oilseed rape cv. Huabu-9	0	x	0	Zhu et al., 2020	China

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Bacillus cereus	rhizosphere isolates from asymptomatic pak choi roots on clubroot infested fields in Songjang district, Shanghai, China	field isolates from *B. campestris* roots from Songjang, China; single spore isolate pathotype P6 of *P. brassicae*, based on Somé et al. (1996)	pak choi (*B. campestris* sp. *chinensis* L.)	0	x	0	Arif et al., 2021	China
Bacillus subtilis	Serenade® ASO soluble liquid concentrate, *Bacillus subtilis* strain QST713	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	x	Peng et al., 2011	Canada
Bacillus subtilis	Serenade ® ASO™ soluble concentrate	not reported	*B. napus* cv. Fortune RR	x	0	0	Lahlali et al., 2011	Canada
Bacillus subtilis	Serenade ® ASO™ soluble concentrate	field isolate from *B. napus* of heavily infested field near Leduc, Alberta, Canada; likely predominantly pathotype 3	*B. napus* cv. Fortune RR	x	0	0	Lahlali et al., 2013	Canada
Bacillus subtilis	Serenade ® ASO™ soluble concentrate	field isolates: pathotypes 3 and 6 (Williams differential set) from Alberta and Muck Crops Research Station, Canada	*B. napus* cv. 46A76; Pioneer Hi-Bred, Shanghai pak choy *B. rapa subsp. chinensis* cv. Mei Qing Choi; Stokes Seeds Ltd	x	0	0	Gossen et al., 2016	Canada
Bacillus subtilis NCD-2	isolated from cotton rhizosphere	not specified, galls from *B. rapa var. pekinensis*	Chinese cabbage	0	x	0	Guo et al., 2019	China
Bacillus subtilis XF-1	rhizosphere isolate of Chinese cabbage from fields with severe clubroot in Guandu District of Kunming, Yunnan Province, China	field isolate from Panlong District, Kunming Municipality, Yunnan, China; pathotype 4 (Williams differential set)	Chinese cabbage Qingdao 83–1	0	x	0	He et al., 2019	China
Bacillus velezensis	rhizosphere isolates from asymptomatic rapeseed roots on clubroot infested fields in Dangyang county, Hubei, China	field isolates from infected rapeseed clubs	oilseed rape cv. Huabu-9	0	x	0	Zhu et al., 2020	China

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Lysobacter antibioticus	*L. antibioticus* 6-B-1, *L. antibioticus* 6-T-4, *L. antibioticus* 13-B-1 applied as crude extract, seed coating or culture broth	not specified, galls from Chinese cabbage	Chinese cabbage cv. Lu Chun Bai No.1	0	x	0	Fu et al., 2018	China
Lysobacter antibioticus	isolates from Chinese cabbage and vegetable rhizosphere soil from Yunnan province, China	field isolates from infested Chinese cabbages in Kunming, Yunnan province, China; dominant: pathotype 4 (Williams DC)	Chinese cabbage cv. Chunxibawang No.1 and Chenzha No.5	0	x	x	Zhou et al., 2014	China
Lysobacter capsici	*L. capsici* ZST1-2 applied as crude extract, seed coating or culture broth	not specified, galls from Chinese cabbage	Chinese cabbage cv. Lu Chun Bai No.2	0	x	0	Fu et al., 2018	China
Microbispora rosea	strains isolated from Chinese cabbage cv. Sam-Bok from various locations, Korea; identified as *Microbispora rosea subsp. rosea*	not reported	Chinese cabbage	0	x	0	Lee et al., 2008	Korea
Paenibacillus kribbensis	strain T-9 isolated from soils in Samcheok, Gangwondo, Korea	not reported	Chinese cabbage	0	x	x	Xu et al., 2014	Korea
Streptomyces sp.	field isolates from infested soil near symptomless plants from Levin, New Zealand	infested field soil from Levin, NZ	Chinese cabbage Wong-Bok	0	x	x	Cheah et al., 2000	New Zealand
Streptomyces alfalfae XY25	strain XY25^{T}	naturally clubroot infested field in Miaoziling Village, Huoshaoping Township, Changyang County, Yichang City, Hubei Province, China	Chinese cabbage	0	0	x	Hu et al., 2021	China

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Streptomyces griseoruber	rhizosphere isolates from symptomless Chinese cabbage on infested fields from Sichuan province, China; strain A316 was most effective and identified as *Streptomyces griseoruber*	field isolates of Chinese cabbage from Xipu, Pxian, China	Chinese cabbage cv. Jian-Chu	0	x	x	Wang et al., 2012	China
Streptomyces griseoviridis	Mycostop® wettable powder	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	0	Peng et al., 2011	Canada
Streptomyces lydicus	Actinovate AG® granules	field isolate and field soil from Alberta, Canada; likely pathotype 3	*B. napus* cv. Fortune RR	x	x	0	Peng et al., 2011	Canada
Streptomyces olivochromogenes	strains isolated from Chinese cabbage cv. Sam-Bok from various locations, Korea; identified as *Streptomyces olivochromogenes*	not reported	Chinese cabbage	0	x	0	Lee et al., 2008	Korea
Streptomyces platensis	strain 3–10	isolate SH	*B. napus*	x	0	0	Shakeel et al., 2016	China
Zhihengliuella aestuarii	rhizosphere isolate of *B. juncea* roots in Fuling, Chongqing, China	field isolate from *B. juncea* from Fuling District, Chongqing, China	*B. juncea* var. Tumida Tsen	0	x	x	Luo et al., 2018a, b	China
Mixture of BCAs								
Bacillus megaterium, Clostridium tyrobutyricum, Saccharomyces cerevisiae	*B. megaterium* (ATCC 14581), *C. tyrobutyricum* (ATCC 25755) and *S. cerevisiae* (ATCC 16664) mix 10^8 CFU/ml	Chinese cabbage galls, dried	*B. rapa ssp. chinensis*	0	x	0	Gao & Xu, 2014	unknown
EM-1	mix of 70 microbial species including bacteria and fungi; applied as 1 l/ha	clubroot-infected cabbage roots, pulverized	oilseed spring rape cv. Trend, white mustard cv. Borowska, white kohlrabi cv. Titan, kale cv. Średniowysoki Zielony Kędzierzawy	0	0	x	Kurowski et al., 2009	Poland

Table 1 (continued)

BCA[a] species	BCA details if available	*P. brassicae* inoculum source	Plant host	CC	GH	FT	Reference	Country
Biochikol 020 PC	applied as seed treatment and seedling disinfection	clubroot-infected cabbage roots, pulverized	oilseed spring rape cv. Trend, white mustard cv. Borowska, white kohlrabi cv. Titan, kale cv. Średniowysoki Zielony Kędzierzawy	0	0	x	Kurowski et al., 2009	Poland
Trichoderma asperellum + Lignohumate AM	Trichoderma identified with ITS4/ITS5 primers, CBS433.97 isolated from a cabbage plantation	not specified	*B. oleraceae var. capitata*	0	0	x	Suada et al., 2019	Indonesia
Trichoderma koningiopsis and dolomite (liming)	isolate Th003 formulated as Tricotec®	infested field soil	*B. oleraceae var. capitata*	0	0	x	Botero et al., 2015	Colombia
Trichoderma harzianum T4 and *Bacillus subtilis* XF-1	*Bacillus subtilis* XF-1, Yunnan Agricultural University, genome sequence CGMCC No. 2357; *Trichoderma harzianum* T4, East China Unversity of Science and Technology	clubs from Chinese cabbage	Chinese cabbage	0	x	0	Yu et al., 2015	China
BactoMix 5	*Bacillus subtilis* V-845 D and V-843 D, *B. megaterium*, *Pseudomonas aurantiaca* and *Brevibacillus* sp.	naturally infested soil	Chinese cabbage var. Granaat	x	0	0	Loit et al., 2020	Estonia
Microbial consortia	Patented biocontrol bacterial strains *Bacillus cereus* BT-23, *Lysobacter antibioticus* 13 – 6, *Lysobacter capsici* ZST1-2	Naturally infested soil around Chinese cabbage, Dabai, China	Chinese cabbage	0	0	x	Zhang et al., 2022	China

[a] Abbreviations: BCA biocontrol agent; CC climate chamber with adjustable, constant temperature conditions; GH greenhouse; FT field trials

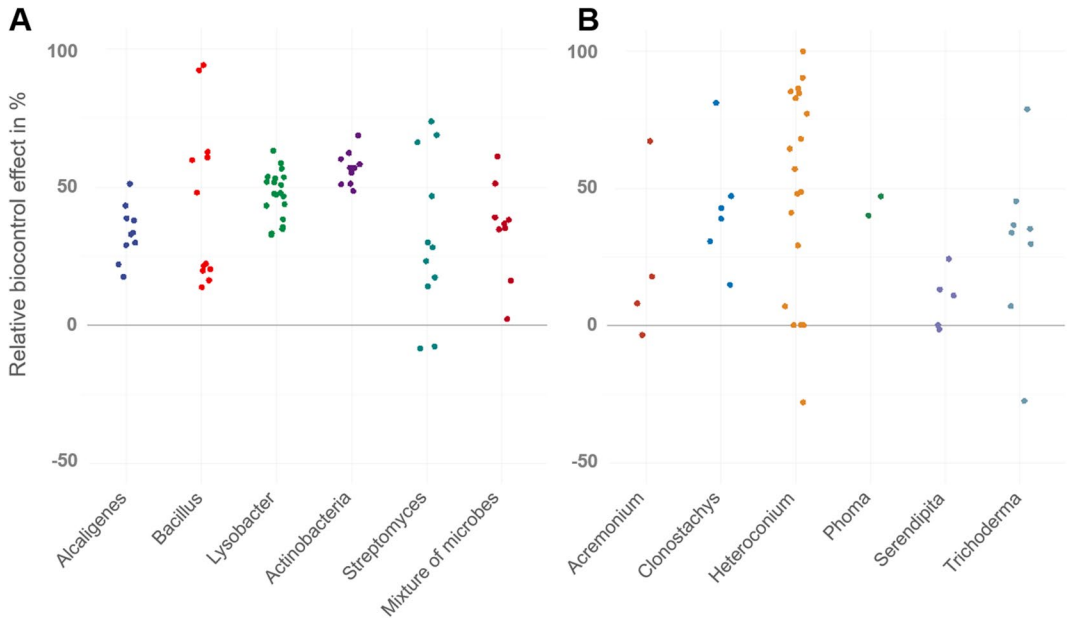

Fig. 1 Overview of the effect of biocontrol agents (BCA) on the Disease Index (DI) of clubroot-infected plants. Shown is the percentage of disease reduction, the relative biocontrol effect, achieved through application of bacterial BCAs (panel **A**) and fungal BCAs (panel **B**) in relation to clubroot-infected plants that did not receive BCA treatment. The relative biocontrol effect was calculated as percentage: 100-DI (plants treated with BCA and clubroot)×100 / DI (plants with clubroot). Genus names used here are those that originate from the literature base for the data presented and do not necessarily present the current phylogenetic status of the BCA. Basis of this graph are 20 studies from Table 1, see Supplement 1 for the data used for this figure

application of many BCAs needs to be optimized, i.e. formulations should be improved if necessary to make them easier to apply, affordable and tested under the specific growing conditions of the target cultivar (Harman et al., 2010; Parnell et al., 2016).

Mechanistic insights into biocontrol of clubroot disease

While many reports describe the mainly positive effect of BCAs for different host—biocontrol combinations, the mechanistic cause was addressed only in a few experimental studies that went beyond the reduction of clubroot, amount of pathogen or additional features that help to increase the effect. We have identified three major possible modes of action: competition, antibiosis through e.g. enzyme secretion like chitinases, induction of plant defense and/or plant endophyte defense mechanisms.

An antibiosis effect would be expected during germination or primary infection while the induction of defense responses could have an effect on all stages of infection, including the secondary infection phase as described in detail below (e.g. Fu et al., 2018; Li et al., 2014; Zhu et al., 2020). Since an antibiosis effect can be measured by rather simple methods, for example by applying organisms or extracts to resting spores of *P. brassicae*, of which the germination rate or viability is determined, these constitute the majority of reports found in the literature.

Mode of Action 1: Competition for space and nutrients.

The competition for space and resources starts in the soil around the roots, in the rhizosphere (Latz et al., 2018). A large number of BCAs show good rhizosphere competence, i.e. they outcompete other microbes in the struggle for nutrients, such as carbon and nitrogen leaked by plant roots, and the ability to enter plant roots and colonize plant tissues. Fungal BCAs could compete for infection sites through the formation of a dense hyphal network around young host roots and thus hinder *P. brassicae* primary zoospores from entering root hairs. Microscopy can help to find the specific sites of inhibition during clubroot

progression, for example whether root hair or cortex invasion is targeted (Zhao et al., 2022; Zhu et al., 2020) or resting spore germination is inhibited (Fu et al., 2018; Zhu et al., 2020).

Several BCAs are able to inhibit root hair colonization by *P. brassicae* and thus hinder the initial start of the disease progression (Arif et al., 2021; Lahlali et al., 2011, 2013; Zhu et al., 2020). A biofungicide that has been on the market for some time contains *Bacillus subtilis* (now renamed *B. amyloliquefaciens*) and is efficient against clubroot of *Brassica napus* (Lahlali et al., 2011, 2013). On the microscopic level this biofungicide seems to inhibit root hair and cortical infection (Lahlali et al., 2011) and mechanistically, the determination of the expression of selected defense genes pointed to the activation of jasmonic acid and ethylene-related defense pathways (Lahlali et al., 2013).

While the competition effect seems more obvious during primary infection, BCAs can also interfere with reproduction during the second part of the infection cycle in the cortex (Lahlali et al., 2011). During the end of the secondary infection, the protist colonizes cortical tissues to produce resting spores, and so completes the life cycle. BCAs can colonize root tissue extensively and thereby restrict the space in which *P. brassicae* can undergo cell extension and extensive resting spore production. *Trichoderma* fungi colonize *Brassica* roots readily and compete for space and nutrients with other microbes, leading to starvation of their competitors (Khalid, 2017). *Trichoderma* sp. secretes cell wall degrading enzymes such as cellulases, chitinases and glucanases that hydrolyze microbial cell walls and could therefore seriously harm the chitin-containing cell walls of *P. brassicae* resting spores (Moxham & Buczacki, 1983; Vinale et al., 2008). Competition for space could also delay the progress of protist development as has been observed with *Acremonium alternatum* in *B. napus* roots (Auer & Ludwig-Müller, 2014) and in *Arabidopsis thaliana* (Jäschke et al., 2010); here, microscopic observations have shown an 'arrest' at the plasmodial stages. The co-inoculated roots had significantly more cells containing mature plasmodia than resting spores, while roots inoculated only with *P. brassicae* at the same time point had more cells with resting spores. The results were corroborated by gene expression analyses for selected *P. brassicae* genes that show a shift of some genes expressed during plasmodial development to later stages, but *A. alternatum* does not inhibit resting spore germination (Jäschke et al., 2010).

Mode of Action 2: Antibiosis

Antibiosis, the production of compounds to outcompete another microbe, has been observed in several studies. If defense is not upregulated, it is often assumed that an antibiosis effect has taken place. *P. brassicae* cannot be cultivated outside of the plant host so a direct inhibitory effect is difficult to measure. General antibiotic effects can be exploited to identify bacterial strains that possess gene clusters for antibiotic synthesis. The resulting information about possible compounds and the clubroot control potential can then be correlated.

The targets for successful early biocontrol using antibiotic effects lie directly after the release of the resting spores into the soil. One possible mechanism is inhibition of the perception of the germination stimulus exuded by the host so that the resting spores will not germinate, while another mechanism targets the chemotaxis by which the zoospores would find their host roots (Amponsah et al., 2021). The flagella of the zoospores could also be direct targets. If these are shed, then the spores cannot move in the soil water and consequently do not reach their host roots. An example of this has been described for the inhibitory effect of *Pseudomonas protegens* on *Chlamydomonas reinhardtii* motility, where treatment with bacteria resulted in deflagellation of the algal cells (Rose et al., 2021), but this has not yet been directly demonstrated for clubroot. Some antagonistic bacteria from the genera *Bacillus*, *Lysobacter* and *Streptomyces* prevent the germination of *P. brassicae* resting spores (Arif et al., 2021; Fu et al., 2018; Lahlali et al., 2011, 2013; Li, 2013; Li et al., 2014; Shakeel et al., 2016; Wang et al., 2012; Zhao et al., 2016; Zhou et al., 2014).

Bacillus genera are able to make a plethora of different antibiotic compounds (Zhu et al., 2020), including several known antifungal compounds, albeit *P. brassicae* is a protist and not a fungus. Li (2013) and Guo et al.(2019) could place the antibiotic effect of *Bacillus subtilis* strains XF-1 and NCD-2 on one compound, fengycin, that was able to reduce clubroot symptoms alone by lysing the resting spores. Fengycin belongs to a class of cyclic lipopetides. Mutant extracts of *B. subtilis* XF-1 with elevated levels of fengycin also increased their effectiveness against *P. brassicae* (Li et al., 2014). Most likely, the mechanism is through destroying the cell walls of resting spores (Li, 2013). Zhao et al. (2016) identified and purified the water-soluble protein PBT1 from *B. subtilis* XF-1, which disrupts the cell wall of resting spores and has a chitinase-like activity.

The genus *Lysobacter* also contains many promising producers of antibiotics or fungicidal components. Therefore, strains or extracts from this genus were successfully tested against *P. brassicae* development or the inhibition of resting spore germination, respectively (Fu et al., 2018). The mechanism of these strains is most likely also through antibiosis, and the genus has further potential yet to be revealed. Taken together, the antibiotic arsenal of compounds against the clubroot pathogen could include specialized metabolites, peptides or proteins.

An indirect yet useful antibiosis effect is the addition of chitin as a soil amendment to enhance the suppressiveness of soils against soil-borne pathogens especially at a stage when they are dormant like *Plasmodiophora* resting spores (Cretoiu et al., 2013; De et al., 2006; Heller et al., 2007; Hjort et al., 2007). The addition of chitin changes the microbial community composition in suppressive soils towards enrichment of chitinolytic microorganisms such as *Streptomyces* and *Pseudomonas* species. *P. brassicae* spores are rich in proteins, lipids and chitin (Moxham & Buczacki, 1983) and can serve as a nutrient source for bacteria which could lower the amount of infectious resting spores considerably as observed in a reduction of clubroot infections in Chinese cabbage and broccoli (De et al., 2006; Heller et al., 2007; Hjort et al., 2007). Heller et al. (2007) investigated a previously clubroot-infested field plot with a 4-year break of *Brassica* cultivation and used a chitin-nitrogen fertilizer to suppress clubroot on the plots. They found an 81% reduction of gall production in broccoli plants at the end of the season in comparison to the control plot without chitin amendment. The regular addition of soil amendments like chitin seems to preserve the suppressiveness of soils over many years and could be a promising long-term strategy against clubroot (Cretoiu et al., 2013).

Mode of Action 3: Induction of plant or plant endophyte defense mechanisms.

Two analyses have provided extensive transcriptomics datasets, one for a bacterium (Luo et al., 2018a, b) and one for a fungus (Auer, 2015). To interpret such results, the effectiveness of the BCA needs to be considered. While with the fungus *Acremonium alternatum* the reduction of clubroot in Arabidopsis was only 15% at a high *P. brassicae* inoculum dose of 2×10^7 spores per plant, the bacterium *Zhihengliuella aestuarii* reduced clubroot symptoms in *Brassica juncea* quite substantially by up to 63% (Auer, 2015; Luo et al., 2018a).

The endophytic fungus *A. alternatum* most likely induces defense responses after challenging the roots of various host plants (Auer & Ludwig-Müller, 2015) which resulted in the reduction of symptoms on Arabidopsis and Chinese cabbage roots (Doan et al., 2010). Auer (2015) showed in a microarray experiment that the defense response is possibly activated via the SA pathway. The defense induction via priming is likely as cell wall extracts of *A. alternatum* induced a reduction of disease symptoms and gene expression responses similar to the living fungus (Auer, 2015).

Transcriptome analysis of *Brassica juncea* roots after co-inoculation of *P. brassicae* and primed by the bacterial biocontrol strain *Z. aestuarii* indicated the upregulation of defense-related genes, among them *PR* genes with different annotations (Luo et al., 2018a, b). The authors compared their results to transcriptome data of a resistant and susceptible *Brassica rapa* line (Chen et al., 2016) to confirm the genes putatively involved in the resistance response. In addition, they reported that both Pattern Triggered Immunity and Effector Triggered Immunity defense pathways were upregulated after treatment of roots with the biocontrol agent. The last set of differentially upregulated genes includes respiratory burst oxidase and mitogen-activated protein kinase (MAPK) cascade genes, as well as cell wall modification genes. They reported the upregulation of the *PR1* gene, a marker for salicylic acid-dependent defense as well as the gene encoding the salicylic acid (SA) receptor *NPR1* (Luo et al., 2018a, b). SA is an inducer of systemic acquired resistance, but also mediates local resistance. *P. brassicae* has a methyltransferase that can methylate SA, possibly leading to the (partial) suppression of that pathway (Ludwig-Müller et al., 2015) since overexpression of this methyltransferase gene in Arabidopsis results in increased susceptibility (Bulman et al., 2019). In line with these observations, plants with elevated SA levels are more resistant to clubroot (Lovelock et al., 2016; Mencia et al., 2022). However, other bacterial strains seem to use different defense pathways to alleviate clubroot symptoms. Good biocontrol results were attributed by Jia et al. (2022) to the involvement of *PR2* and *EIN3* expression, after treatment of *P. brassicae*-inoculated Chinese cabbage roots with *Alcaligenes faecalis* Juj3.

The two genes indicate that next to SA the ethylene response pathway has to be involved.

The induction of antioxidative enzymes can also contribute to stress resistance and may contribute to the biocontrol effect of a *Bacillus cereus* strain against clubroot of pak choi (Arif et al., 2021). The authors found an increase in catalase, superoxide dismutase and peroxidase activities in roots treated with the BCA and *P. brassicae* compared to *P. brassicae* alone. However, peroxidases can also be involved in plant defense responses (Almagro et al., 2009).

The effect of a biocontrol fungus, *Heteroconium chaetospira*, was analyzed by Lahlali et al. (2014) on *B. napus* clubroot development. In a similar setup as used for Serenade (*Bacillus subtilis*), they determined a selection of defense marker genes and found that jasmonic acid and ethylene-related defense pathways were upregulated. Another commercial biofungicide (Prestop) consisting of a fungus, *Clonostachys rosea*, also showed efficient control against clubroot by using the defense induction of jasmonic acid and ethylene pathways in addition to an antibiosis effect (Lahlali & Peng, 2014). It could be that other pathways are also involved but the respective genes were not within the selection.

Taken together, both types of defense pathways seem to play a role in the reduction of disease symptoms by endophytes.

The role of soil properties and microbiomes

Abiotic soil properties such as moisture and pH have been found to affect the outcome of biocontrol experiments and influence the reduction of clubroot (Gossen et al., 2016). For example, *Heteroconium chaetospira* was only able to reduce clubroot under a certain moisture regime (Narisawa et al., 2005). Furthermore, the authors reported that commercial horticultural soils often contain excess nutrients and retard the growth of endophytic fungi thus exerting negative effects for certain BCAs (Narisawa et al., 2005). If the soil properties need to be individually adjusted this would not make biocontrol popular. Gossen et al. (2016) used four different soil types to test alterations in the efficacy of commercial BCAs, *B. subtilis* and *C. rosea*. The biopesticide Prestop (*C. rosea*) was often more effective than Serenade (*B. subtilis*) at reducing clubroot levels on peat and mineral soils, but less effective than Serenade on sand. They concluded that such variations could explain why biocontrol works in some areas, but not in others (Gossen et al., 2016). In addition, they reported that the soil density also affected the outcome, namely that more compact soil was less favorable for biocontrol effects.

Living organisms in the soil, the rhizobiome and microbiome predators such as other protists, nematodes and arthropods can all influence the survival and therefore establishment and efficacy of biocontrol microorganisms against clubroot through competition, antibiosis or predation. So far, hardly anything is known about this complex topic in regard to clubroot, yet a recent study showed nonspecific consumption of *P. brassicae* resting spores by other protists (Schwelm et al., 2023).

The phytobiome of host plants as well as the soil microbial diversity influences the efficacy of biocontrol and likely the mechanisms involved (Daval et al., 2020; Yu et al., 2015; Zhang et al., 2022; Zhao et al., 2017). For example, *Trichoderma harzianum* isolates were able to increase the number of *Bacillus* strains in the rhizosphere of Chinese cabbage that reduced clubroot incidences (Li et al., 2020) and which may contribute via antibiosis and / or defense priming to clubroot tolerance (Lahlali et al., 2011, 2014). Hu et al. (2021) also attributed the biocontrol effect of a *Streptomyces alfalfae* strain to changes in the microbiome. They not only identified bacteria, but also many fungal genera enriched during *Streptomyces* treatments so the effect cannot be attributed only to enrichment of one organism.

Concluding remarks

The potential of beneficial microbes in pest management against clubroot disease is huge. During our literature research we came across several additional non-peer reviewed sources specifically from South America and Asia that did not make it into this review. This shows that researchers and farmers across the globe test out and use biocontrol against clubroot at likely a much larger scale than the peer-reviewed literature suggests. Unfortunately, the success of such attempts is hard to assess. It is also likely that there is a strong bias toward only effective attempts making it into the citable literature body, thus concealing negative results against clubroot disease that would be equally valuable for the scientific community.

Our literature review shows that the majority of studies used greenhouse or field conditions to assess the efficiency of biocontrol. Not surprisingly, the extent of clubroot control in the field will always depend on other biotic and abiotic factors in the soil such as the persistence of BCAs in the rhizosphere of target plants and their ability to colonize the plant roots sufficiently. Only rhizosphere competent BCAs should be considered for widespread application (Niu et al., 2020). Furthermore, the mode of application of BCAs will be a critical factor in their success and crucial for the economic feasibility of this biocontrol approach. As long as the organisms are not persistent in the field or their application is expensive and economically unfeasible, the BCA-based measures will not provide value over traditional control methods. Another promising approach is to use microbial consortia in the field against clubroot (Niu et al., 2020; Zhang et al., 2022). It will remain crucial to maintain soil health, nutrient availability and good soil structure for optimal plant growth and efficient recruitment of plants for the endophytes that will benefit the plant.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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