E-ISSN: 2618-0618
P-ISSN: 2618-060X

www.agronomyjournals.com
2024; 7(4): 577-583
Received: 06-02-2024
Accepted: 16-03-2024

Richard Ntakirutimana
Department of Plant Pathology, Lovely Professional University, Jalandhar, Delhi, India

Jacqueline Ishimwe
Department of Crop Sciences, College of Agriculture, Animal Sciences and Veterinary Medicine (CAVM), University of Rwanda, Rwanda

Josee Ukobukeye
Department of Genetics &Plant Breeding, Institute of Agricultural Sciences, Siksha 'o' Anusandhan University, Bhubaneswar, Odisha, India

Corresponding Author:
Richard Ntakirutimana
Department of Plant Pathology, Lovely Professional University, Jalandhar, Delhi, India

Multiple-strain biological control agents and their impact on soil borne plant diseases

Richard Ntakirutimana, Jacqueline Ishimwe and Josee Ukobukeye

DOI: https://doi.org/10.33545/2618060X.2024.v7.i4h.607

Abstract
Soilborne plant pathogens cause significant crop losses worldwide. The use of biological control agents (BCAs) to suppress plant diseases has gained much interest as an alternative to chemical pesticides. Single-strain BCAs have demonstrated efficacy against some soilborne pathogens, but multiple-strain mixtures may provide greater and more consistent disease control. This review examines current research on Multiple-BCA strain mixtures, including their mechanisms of action, compatibility, field efficacy, and potential risks. Numerous studies indicate mixtures can provide broad-spectrum suppression through complementary and synergistic interactions among strains. Compatibility testing protocols have enabled the development of effective multi-strain products. Field trials demonstrate these products often perform comparably or better than single strains or chemical fumigants. However, further research optimizing the formulation, delivery, and environmental fit of mixtures is needed. Ultimately, multi-strain BCAs offer a promising sustainable tool for the integrated management of soilborne crop diseases.

Keywords: Soilborne pathogens, biological control, biopesticides, disease suppression, microbial mixtures, multi-strain inoculants, integrated pest management, plant diseases, soil microbiome, field efficacy

Introduction

Soilborne fungal, oomycete, bacterial, and nematode phytopathogens are responsible for major economic crop losses worldwide. Diseases caused by soilborne pathogens are difficult to control due to the pathogens' persistence in soil and other environmental reservoirs [1]. Fumigation with broad-spectrum biocides has traditionally been an effective method to reduce inoculum potential of pathogen propagules in soil. However regulatory restrictions, rising costs, public health concerns, and negative environmental impacts have greatly limited fumigant use [2, 3]. This has driven investigation of alternative non-chemical approaches for soilborne disease management, including cultural practices, resistant cultivars, and biological control.

Biological control through introduction of antagonistic microorganisms has shown particular promise as a sustainable, eco-friendly means to protect plants from soilborne diseases [4]. Numerous bacterial and fungal biological control agents (BCAs) have been identified that can suppress various soilborne pathogens via competition, antibiosis, parasitism, induced resistance, and other mechanisms [5]. Commercial microbial pesticides based on single antagonistic strains, such as species of *Bacillus*, *Streptomyces*, *Trichoderma*, and *Gliocladium*, have demonstrated efficacy in controlling certain soilborne diseases under field conditions [6–9]. However, biological control efficacy using single antagonists can be inconsistent due to variability in environmental conditions, pathogen pressure, and crop cultivar [10–12]. As soilborne plant pathogens often have broad host ranges, utilize multiple infection strategies, and produce resilient resting structures, targeting them with single antagonist strains poses challenges [1, 13].

One proposed method to overcome such limitations is through use of mixtures of multiple complementary BCAs. Evidence from interactions of pathogens and native soil microbiota suggests multi-species communities play an integral role in disease-suppression [14–16]. Introducing combinations of selected antagonists may more closely mimic native suppressive microbiomes. Theoretically, mixtures of BCAs with different mechanisms of action, environmental fitness, and/or target pathogens could provide more consistent, broader spectrum control [17–21].

Most commercial BCAs consist of single isolates, but interest in developing multi-strain mixtures has grown recently. Several mixed inoculant products have shown promising results in suppressing soilborne crop diseases under field conditions [22–25]. This review synthesizes current knowledge on multi-strain BCAs for managing soilborne pathogens, examining mechanisms of disease suppression, compatibility among strains, field efficacy results, and potential risks associated with their use.

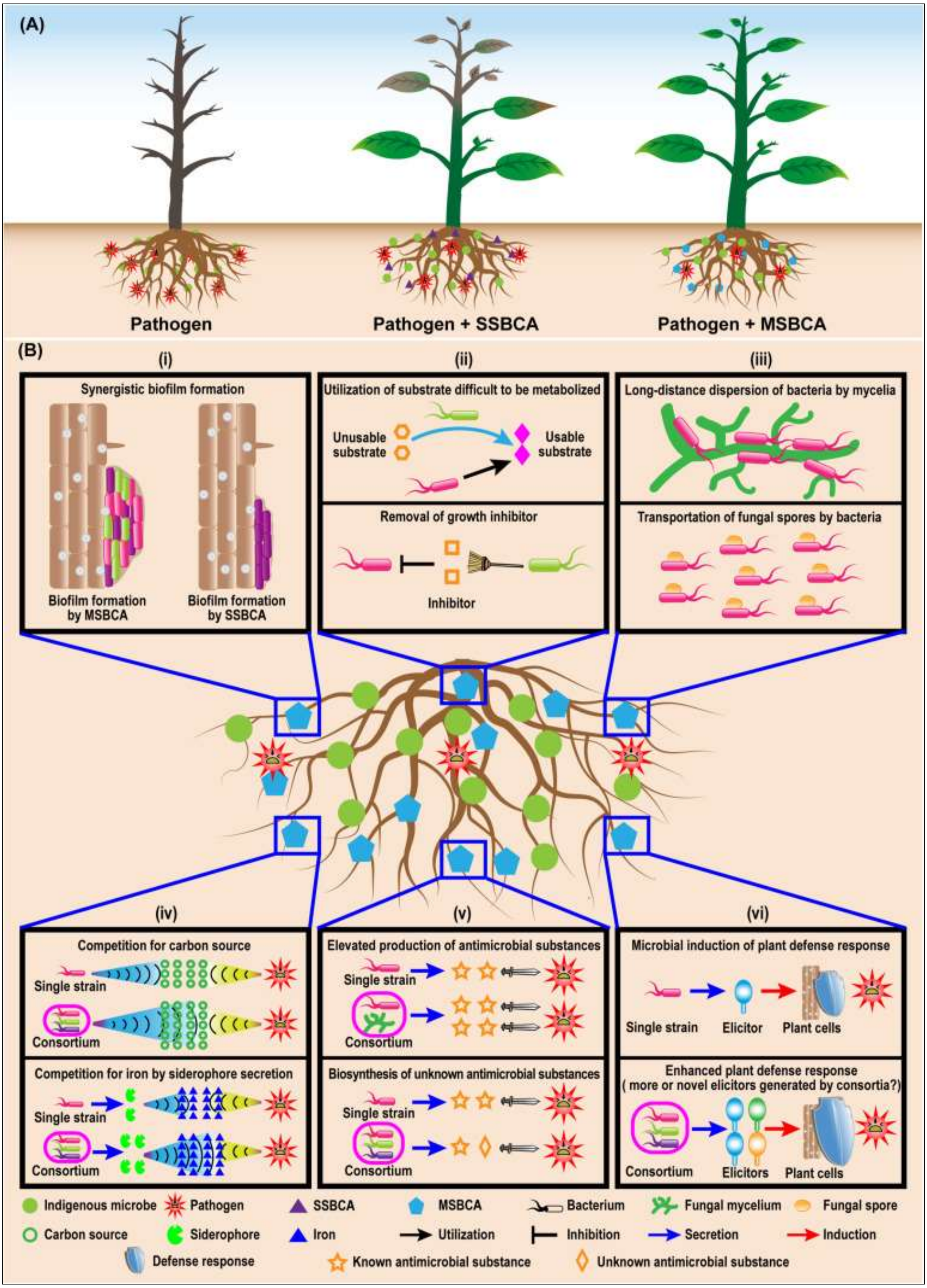

Fig 1: Increased disease-suppressive efficacy (B) and enhanced biocontrol effects (A) of multiple-strain biological control agents (MSBCA) against soil-borne pathogens. The following effects have been observed: (i) increased biofilm formation; (ii) encouragement of syntrophic microbial growth; (iii) facilitated migration; (iv) increased competition for resources; (v) encouraged the manufacture of antimicrobial substances; and (vi) heightened activation of plant defense response [66]

Mechanisms of disease suppression

Introducing combinations of microbial antagonists may enable greater pathogen control through additive, synergistic interactions or complementary mechanisms of action targeting different pathogens or disease stages. Proposed benefits include (i) increasing taxonomic and functional diversity, (ii) resource partitioning and efficiency, (iii) stabilizing antagonistic populations over time and space; and (iv) providing general and specific suppression abilities [26]. Mixed inoculants may also allow for lower application rates of individual strains needed to achieve disease control. Table 1 summarizes known biocontrol mechanisms employed among common BCA groups used in multi-strain approaches against soilborne pathogens.

Table 1: Mechanisms of biological control among major microbial antagonists used in multi-strain mixtures for suppression of soilborne crop diseases

Microbial Group	Bacteria	Fungi	Protozoa
Taxa Examples	Bacillus spp., Pseudomonas spp., Streptomyces spp.	Trichoderma spp., Metarhizium spp., Beauveria spp.	Myxamoeba spp., Acanthamoeba spp., Naegleria spp.
Mechanisms	Antibiosis, Competition, Enzyme secretion, Induced resistance	Mycoparasitism, Antibiosis, Competition, Enzyme secretion	Predation, Competition, Induced resistance
Target Pathogens	Broad spectrum of bacterial & fungal pathogens	Broad spectrum of fungal pathogens	Nematodes, fungi, oomycetes
Commercial Products	Serenade, Double Nickel, Actinovate	Soil Gard, Root Shield, Actinovate	Nemout, Nemaseek

Introducing diverse bacteria, fungi, nematodes, or other microbes may lead to niche partitioning where strains utilize different carbon sources or colonize different ecological zones (e.g rhizosphere vs endorhiza), enabling more efficient use of resources [27, 28]. Varying survival and activity of strains over time can also stabilize population densities to exert continual pathogen pressure. Additionally, general suppression from heightened microbial activity can complement targeted inhibition of key pathogens [29]. Broadly, three models describe potential interactions of multi-strain mixtures: additive, synergistic, or antagonistic [30].

Additive/complementary interactions

In an additive interaction, disease control is equal to the sum of activities from the individual strains applied separately. This occurs when mixtures target different pathogens, niches, or stages of the disease cycle without directly interacting. Mixtures of bacteria or fungi strains having distinct inhibition mechanisms can provide broad, complementary control across multiple diseases [31].

Synergistic interactions

Synergy refers to mixtures giving greater control than the additive effects of its components [32]. Positive microbial interactions enhancing biocontrol include co-metabolism of substrates, stress resistance, or detoxification of pathogen metabolites [33]. Signal molecules among strains may stimulate antibiotic production or trigger induced systemic resistance pathways [34]. Specific combinations have shown synergistic mycoparasitism, where enzymes from one antagonist facilitate penetration and attack of pathogens targeted by another [35].

Antagonistic interactions

Detrimental inhibitory interactions can also occur between co-inoculated microbes competing for limited nutrients and space, leading to impaired biocontrol [36]. Production of volatile organic compounds, antibiotics, or pH altering metabolites may directly inhibit other BCA strains [37]. The net effect of mixed inoculation depends on relative synergistic, additive and antagonistic interactions. Compatibility testing helps avoid major antagonism among strains.

Several studies demonstrate multi-strain mixtures suppressing soilborne pathogens through presumed synergistic or complementary effects in greenhouses, growth chambers, and field tests. Yang *et al.* [38] found combinations of Bacillus subtilis, *B. amyloliquefaciens*, *B. cereus*, and *B. pumilus* led to significantly greater inhibition of *Fusarium oxysporum* f. sp. niveum and *Ralstonia solanacearum* on watermelon over single applications. They observed increased production of antifungal lipopeptides and siderophores among certain paired combinations, suggesting synergistic interactions. Cross protection and degradation of toxins may also occur, as Kelley and Gilbert [39] reported mixtures of Bacillus strains provided greater control of Pythium damping off than individuals possibly by removing metabolites inhibiting growth. In radish root microbiome studies, Streptomyces-Bacillus combinations gave broad-spectrum disease suppression against *F. oxysporum*, *Rhizoctonia solani*, and *R. solani* AG-2-1 not achieved with singles [40]. The diverse inhibitory metabolites among these taxa likely contributed to complementary activity.

Combinations of fungi have also shown multifunctional control, as Trichoderma-Gliocladium mixtures reduced pathogens inciting damping-off, root, stem and fruit diseases on several hosts [41, 42]. Enhanced antibiotic production was noted between *Trichderma harzianum* and *T. viride* strains [43]. Specific mycoparasitic Trichoderma species combinations can attack different stages of pathogens' life cycles [35]. Joint inoculation with Rhizobacteria and Trichoderma strains has provided consistent biocontrol and plant growth enhancement by stimulating systemic resistance pathways in both associates and the host plant [44–46]. Findings support the hypothesis mixtures enable greater disease suppression through synergistic population dynamics and mechanisms. However additive or antagonistic interactions may also predominate depending on the strains and environments. Further work is still needed to demonstrate disease reduction by multi-strain BCAs is due directly to additive, synergistic or complementary effects rather than chance through increased probability of one effective antagonist.

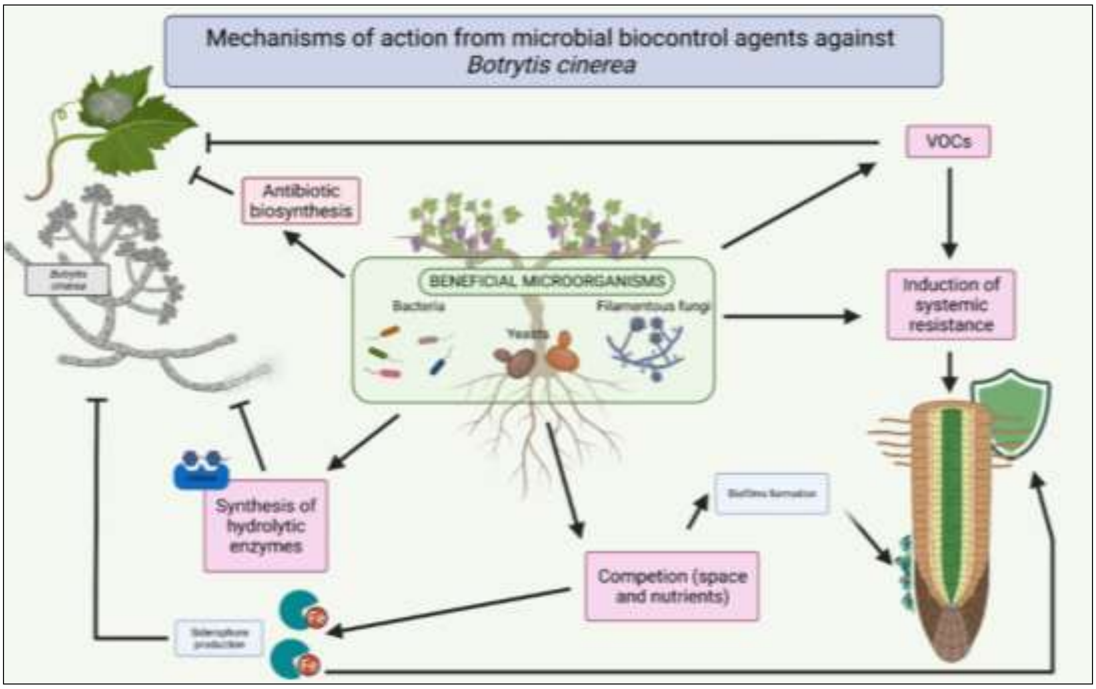

Fig 2: Mechanisms of action of microbial biocontrol agents against Botrytis cinerea

Compatibility among strains

Introducing antagonistic microbes together risks potential antagonism detrimentally affecting biocontrol efficacy. Thus compatibility among candidate BCA strains should first be established to avoid selecting incompatible partners. Approaches to assess compatibility include: direct inhibitory assays on dual culture media, analysis of interactions effects on fungal/bacterial morphology and metabolism, plant inoculation assays, selective desirability functions, studying enzyme activities post-interaction, and PCR community profiling [30, 47].

Plate assays offer an initial screen for strongly antagonistic or potentially synergistic interactions among strains [48]. Partners showing no growth inhibition are then further tested in greenhouse bioassays on plants. Additive or synergistic disease suppression effects in such trials indicates general compatibility of the mixture. Observing consistent control efficacy of mixtures applied over multiple field seasons provides the best validation of strain compatibility and stability [49].

Researchers utilize various statistical approaches to select optimal strain combinations from initially large pool of candidates, including desirability functions, mixture simplex lattice design modelling, and the 'Bacterial Complementation' (BACO) screening method [30, 50, 51]. Compatibility testing plays a key role in commercial development of multi-strain inoculants allowing manufacturers to formulate stable, reliable products. Most available mixed BCA products feature combinations of Bacillus spp., with some integrating Trichoderma or Streptomyces strains (see Table 2). Combining fungi and bacteria poses greater risks for antagonistic interactions due to differing nutritional needs and potential production of anti-fungal or anti-bacterial compounds [52]. Yet examples of bio-compatible mixed inoculants exist, such as Sentinel containing both Trichoderma and Bacillus strains. Identifying mutually supporting, ecologically suited combinations remains an active area of research.

Table 2: Examples of commercially available multi-strain biological control products for suppression of soilborne crop diseases

Product	Strains	Target Pathogens	Crops
Double Nickel LC/WDG	Bacillus amyloliquefaciens strain D747 + other proprietary Bacillus spp.	Fungal pathogens including *Fusarium*, *Rhizoctonia*, *Phytophthora*, *Pythium*, etc.	Wide range of fruit, vegetable, grain and ornamental crops
Serenade SOIL	Bacillus subtilis strain QST713 + Bacillus pumilus strain INR7	Seedling diseases, root rots, wilts	Vegetables, fruits, row crops
Bio-Nematon + Actinovate SP	Steinernema feltiae nematode + Streptomyces lydicus WYEC108	Root-knot nematodes, soilborne fungal pathogens	Vegetables, fruits, ornamentals
Sentinel	*Trichoderma harzianum* strain KRLAG2 + Bacillus subtilis strain OSU142	Fusarium, Rhizoctonia, Pythium diseases	Soybeans

Field efficacy

Ultimately, the efficacy of potential BCA mixtures must be validated under field conditions over multiple sites and seasons. Environmental factors like soil type, temperature, moisture, nutrient levels, and indigenous microbiota can modulate biocontrol activity [53]. While mixtures often show disease suppression in controlled settings, performance consistency has been a key limitation during field deployment [10]. Multi-strain inoculants aim to provide more reliable broad-spectrum control via built-in functional redundancy among strains.

A number of recent long-term studies have demonstrated certain mixtures adequately controlling targeted soilborne pathogens. Conn *et al.* [24] tested various bacterial combinations against cabbage yellow caused by *F. oxysporum* f. sp. conglutinans for five years in Alaska. Treatments with Bacillus subtilis paired with B. megaterium, B. simplex or B. cereus consistently provided disease suppression comparable to standard fungicide and fumigation benchmarks across all trial years. Mixture efficacy was additive or synergistic rather than through one strain dominating. Sarhan *et al.* [25] similarly found potato yield enhancement from combining B. subtilis and B. megaterium strains to minimize Rhizoctonia canker and black scurf matched standard pesticide over three seasons. Greenhouse assays suggested biocontrol activity resulted from synergistic interactions between the two strains.

Investigating multi-year onion white rot suppression by Pseudomonas and Bacillus combinations, McLean *et al*. [22] determined strain J636 (P. fluorescens) was the most efficacious single BCA. Y*et al*ternating or mixing J636 with other bacteria gave optimal control and yield response. This was attributed to the mixtures conferring stronger, more consistent population levels in the rhizosphere to withstand environmental variability. The nematode-attacking fungus Hirsutella Rhossiliensis also shows greater reliability for controlling root-knot nematodes during field applications when integrated with Paecilomyces lilacinus over four seasons [54]. Though individual H. rhossiliensis applications could equal mixtures, its parasitism was less stable between years. These examples demonstrate key benefits of multi-strain inoculants in conferring predictable broad-spectrum protection.

Yet other long-term trials show single antagonist isolines providing equivalent if not greater soilborne disease control than mixtures. In BCA tests against Phytophthora blight of bell pepper over seven years, individual strains of Bacillus, Streptomyces and chitosan outperformed commercial mixed inoculants [55]. This indicated compatibility issues may have reduced field efficacy of the mixtures. For suppressing lettuce drop caused by Sclerotinia minor, rotations of Streptomyces lydicus with fungicides proved a more consistent strategy than applying S. lydicus mixtures [56]. Synergistic interactions enhancing biocontrol likely depend on specific strain combinations as well as environmental conditions.

While existing commercial products rely largely on combinations of Bacillus spp., mixtures integrating diverse bacteria, fungi, yeasts or other microbes may provide better occupation of soil niches for disease suppression. Future field investigations should further explore broad taxonomic combinations using isolates native to deployment regions. Multi-strain inoculant research also requires greater attention to appropriate formulation, storage, delivery methods and application rates for maintaining stability [57]. As strains likely utilize different substrates, varied nutritional requirements must be met to retain viability and efficacy.

Potential risks

Despite demonstrated benefits for soilborne disease control, uncertainties around environmental and health risks associated with introducing non-native microbiota provide reasonable rationale for caution adopting multi-strain inoculants [58]. Potential concerns include altered soil ecology leading to loss of biodiversity or enrichment of new pathogens, production of harmful metabolites, gene transfer to native microbes, excessive nutrient competition with plants, or risks to human end users [23, 59]. Realizing such negative impacts seems unlikely for most candidate BCA groups which originate from soil environments similar to deployment areas. Still, non-target effects must be considered, especially when applying combinations of genetically modified strains [60].

Few studies directly analyze ecological impacts from long-term use of multi-strain inoculants. Transitioning to organic methods with reduced pesticide inputs increased general soil health and biodiversity in certain farm systems while utilizing applications of composts, microbial amendments, and other alternative disease management products containing mixed microbes [61–63]. This suggests integrative biological approaches unlikely drastically disrupt soil ecology. Targeted community analysis via next generation sequencing could clarify effects of introducing persistent high levels of BCA inoculants on indigenous microbial populations [64]. Monitoring population dynamics of inoculant strains compared to the native microbiome would provide valuable information on environmental fate, gene transfer risks, and community impacts associated with long term usage of multi-strain BCA mixtures [65].

Conclusions and future outlook

In conclusion, introducing combinations of microbial biological control agents holds promise as a more reliable sustainable approach for managing endemic soilborne crop diseases over single strain alternatives. Multi-strain inoculants provide broad-spectrum suppression through increased taxonomic, genetic and functional diversity and varying modes of antagonistic action. Field investigations demonstrate certain mixtures effectively controlling fungal, bacterial, nematode and oomycete plant pathogens. Combining strains with complementary inhibition mechanisms can lead to additive or synergistic interactions improving biocontrol efficacy. Yet performance consistency depends on selecting mutually compatible BCAs through rigorous antagonism and bioassay testing to avoid counterproductive microbial interactions. Control efficacy also relies on proper product formulation and application methods tailored to constituent strains' environmental requirements.

Further research should explore novel combinations integrating diverse bacteria, fungi, nematodes or protozoa co-adapted from disease suppressive soils which may occupy distinct niches. Native isolates pre-selected for synergistic interactions could offer enhanced control once combined. Continued field testing over multiple locations and years will clarify most robust mixtures for commercialization. Multi-strain inoculants provide an additional tool for integrated pest management programs seeking to reduce conventional pesticide applications. Realizing the full potential of tailored microbial consortia to sustainably suppress soilborne crop diseases will require ongoing interdisciplinary investigation between microbial ecologists, plant pathologists and biological control researchers.

References

1. Baker KF, Cook RJ. Biological Control of Plant Pathogens. San Francisco, CA: WH Freeman and Company; 1974.
2. Ajwa H, Trout T, Mueller J, Wilhelm S, Nelson S, Soppe R, Shatley D. Application of alternative fumigants through drip irrigation systems. Phytopathology. 2002;92:1349-1355.
3. Csinos AS, Stephenson MG, Walker A. Evaluation of brassica spp. As winter cover crops for weed control in plastic mulch vegetable production. Crop Prot. 2016;89:29-33.
4. Campbell R. Biological control of microbial plant pathogens. Cambridge: Cambridge University Press; 1989.
5. Compant S, Duffy B, Nowak J, Clément C, Barka EA. Use of plant growth-promoting bacteria for biocontrol of plant diseases: Principles, mechanisms of action, and future prospects. Appl Environ Microbiol. 2005;71:4951-4959.
6. Chen Z, Wang B-J, Li J-Q, Zhu J-H, Ren C-G. Effects of Streptomyces griseorubens JSD-1 on Fusarium wilt and soil microbial communities in successive banana monoculture soils. Crop Prot. 2019;124:104898.
7. Won Kang S, Seong Mun S, Seok Kim Y. Management of rhizoctonia root rot in ginseng with multifunctional

Trichoderma harzianum AD12. Plant Pathol J. 2019;35.
8. Abdallah RAB, El Mohamedy RSR, Jabnoun-Khiareddine H, Daami-Remadi M, Hibar K, Khiareddine HJ-, El Mahjoub M. Biocontrol efficacy of Bacillus subtilis strains HQ 916603 against Fusarium oxysporum f. sp. radicis-cucumerinum the causal agent of Fusarium crown and root rot of cucumber. Biol Control. 2016;97:29-36.
9. Stewart A, Ajwa H, Nava-Juarez R, Qin R, Vaughn SF. GL21 fertilizer, AM-fungi and PGPR combinations suppress the soilborne pathogen complex, increase yield and improve fruit quality in replanted strawberry under low and high disease conditions. Plant Dis. 2018;102:2554-2564.
10. Bashan Y, de-Bashan LE, Prabhu SR, Hernandez JP. Advances in plant growth-promoting bacterial inoculant technology: Formulations and practical perspectives (1998–2013). Plant Soil. 2014;378:1-33.
11. Guetsky R, Shtienberg D, Elad Y, Fischer E, Dinoor A. Improving biological control by combining biocontrol agents each with several mechanisms of disease suppression. Phytopathology. 2002;92:976-985.
12. Stewart A. Redefining the mechanism by which biocontrol products improve crop health and productivity under conditions of biotic stress. Biocontrol Sci. Technol. 2017;27:1353-1365.
13. Thomashow LS, Weller DM. Current concepts in the use of introduced bacteria for biological disease control: Mechanisms and antifungal metabolites. In: Plant-Microbe Interactions; Boston, MA: Springer; c1988. p. 187-235.
14. Garbeva P, van Veen JA, van Elsas JD. Microbial diversity in soil: Selection of microbial populations by plant and soil type and implications for disease suppressiveness. Annu. Rev. Phytopathol. 2004;42:243-270.
15. Pierson EA, Weller DM. Use of mixtures of fluorescent pseudomonads to suppress take-all and improve the growth of wheat. Phytopathology. 1994;84:940-947.
16. Domenech J, Reddy MS, Kloepper JW, Ramos B, Gutierrez-Manero J. Combined application of the biological product LS213 with Bacillus, Pseudomonas or Chryseobacterium for growth promotion and biological control of soil-borne diseases in pepper and tomato. BioControl. 2006;51:245-258.
17. Jetiyanon K, Kloepper JW. Mixtures of plant growth-promoting rhizobacteria for induction of systemic resistance against multiple plant diseases. Biol. Control. 2002;24:285-291.
18. McLean KL, Swaminathan J, Stewart A. Increasing soil ecosystem services through effective management of introduced microbial agents: Challenges and opportunities. Appl. Soil Ecol. 2012;61:356-366.
19. Bashan Y. Risks of using recombinant biocontrol microbes: Challenges and solutions. Phytoparasitica. 2018;46:317-326.
20. Conn VM, Qian C, Durkin J. Combinations of Streptomyces sp. strains provide greater biocontrol of cabbage head rot (*Fusarium sambucinum*) than individual strains alone. Plant Dis. 2018;102:2063-2067.
21. Sarhan ARY, Hamza MA, Youssef HH, Patz S, Becker JO, El Saied AE-SM. Synergistic interaction of endophytic Bacillus spp. and *Trichoderma harzianum* S.L. In the biocontrol of Cucumber wilt disease. Front Bioeng Biotechnol. 2019;7:17.
22. Brewer MT, Larkin RP. Efficacy of several potential biocontrol organisms against *Rhizoctonia solani* on potato. Crop Prot. 2005;24:939-950.
23. Gu G, Cevallos-Cevallos JM, Vallad GE, van Bruggen AHC. Organically managed soils reduce internal colonization of tomato plants by Salmonella enterica serovar typhimurium. Phytopathology. 2012;102:381-388.
24. Penton CR, Johnson TA, Quensen JF, Iwai S, Cole JR, Tiedje JM. Functional genes to assess nitrogen cycling and aromatic hydrocarbon degradation: Primers and processing matter. Front Microbiol. 2013;4:279.
25. Alabouvette C. Fusarium-wilt suppressive soils: An example of disease-suppressive soils. Australas Plant Pathol. 1999;28:57-64.
26. Dunne C, Moenne-Loccoz Y, McCarthy J, Higgins P, Powell J, Dowling D, Gara FO. Combining proteolytic and phloroglucinol-producing bacteria for improved biocontrol of Pythium-mediated damping-off of sugar beet. Plant Pathol. 1998;47:299-307.
27. Guetsky R, Shtienberg D, Elad Y, Fischer E, Dinoor A. Combining biocontrol agents to reduce the variability of biological control. Phytopathology. 2002;92:621-627.
28. Crowe FJ, Olsson S. Induction of laccase activity in *Rhizoctonia solani* by antagonistic Pseudomonas fluorescens strains and a range of chemical treatments. Appl. Environ Microbiol. 2001;67:2088-2094.
29. Molina L, Constantinescu F, Michel L, Reimmann C, Duffy B, Défago G. Degradation of pathogen quorum-sensing molecules by soil bacteria: A preventive and curative biological control mechanism. FEMS Microbiol Ecol. 2003;45:71-81.
30. Cortés-Barco AM, Goodwin PH, Hsiang T. Induced systemic resistance against three foliar diseases of Agrostis stolonifera by (2R, 3R)-butanediol or an isoparaffin mixture. Ann Appl Biol. 2010;157:179-189.
31. de Boer W. Upscaling of fungal–bacterial interactions: From the lab to the field. Curr Opin Microbiol. 2017;37:35-41.
32. Alavi P, Starcher MR, Zachow C, Müller H, Berg G. Root microbiome dynamics of perennial Arabis alpina are dependent on soil residence time but independent of flowering time. Microbiome. 2018;6:1-15.
33. Yang JW, Yi HS, Kim H, Lee B, Lee S, Ghim SY, *et al*. Whitefly infestation of pepper plants elicits defence responses against bacterial pathogens in leaves and roots and changes the below-ground microflora. J Ecol. Entomol. 2011;104:14-20.
34. Kelley K, Gilbert J. Bacillus cereus UW85 inoculation effects on growth, seed yield, and disease control of common beans under greenhouse conditions. Hort. Science. 2003;38:242-246.
35. Lee B, Lee S, Ryu CM. Foliar aphid feeding recruits rhizosphere bacteria and primes plant immunity against pathogenic and non-pathogenic bacteria in pepper. Ann Bot. 2012;110:281-290.
36. Spadaro D, Droby S. Development of biocontrol products for postharvest diseases of fruit: The importance of elucidating the mechanisms of action of yeast antagonists. Trends Food Sci. Technol. 2016;47:39-49.
37. Woo SL, Scala F, Ruocco M, Lorito M. The molecular biology of the interactions between Trichoderma spp., phytopathogenic fungi, and plants. Phytopathology. 2006;96:181-185.
38. Sivan A, Chet I. Integrated control of Fusarium crown and root rot of tomato with *Trichoderma harzianum* and methyl bromide. Crop Prot. 1993;12:380-386.
39. Altomare C, Norvell WA, Bjorkman T, Harman GE.

Solubilization of phosphates and micronutrients by the plant-growth-promoting and biocontrol fungus *Trichoderma harzianum* Rifai 1295-22. Appl. Environ Microbiol. 1999;65:2926-2933.
40. Shoresh M, Harman G, Mastouri F. Induced systemic resistance and plant responses to fungal biocontrol agents. Annu Rev Phytopathol. 2010;48:21-43.
41. Singh R, Shelke G, Kumar A, Jha P. Biochemistry and genetics of ACC deaminase: A weapon to "stress ethylene" produced in plants. Front Microbiol. 2015;6:937.
42. Dunne C, Crowley JJ, Moënne-Loccoz Y, Dowling DN, de Bruijn FJ, O'gara F. Biological control of *Pythium ultimum* by *Stenotrophomonas maltophilia* W81 is mediated by an extracellular proteolytic activity. Microbiology. 1997;143:3921-3931.
43. Raupach GS, Kloepper JW. Mixtures of plant growth-promoting rhizobacteria enhance biological control of multiple cucumber pathogens. Phytopathology. 1998;88:1158-1164.
44. Jetiyanon K, Fowler WD, Kloepper JW. Broad-spectrum protection against several pathogens by PGPR mixtures under field conditions in Thailand. Plant Dis. 2003;87:1390-1394.
45. Dunne C. Biological control of cavity spot of carrot (*Daucus carota*) caused by Pythium spp. Ph.D. Thesis, University College Cork, Ireland; December 1998.
46. Matos A, Kerkhof L, Garland J. Effects of microbial community diversity on the suppressiveness of rhizosphere microbiomes to bacterial canker of tomato. Phytopathology. 2005;95:235-241.
47. Frey-Klett P, Garbaye J, Tarkka M. The mycorrhiza helper bacteria revisited. New Phytol. 2007;176:22-36.
48. Bashan Y, de-Bashan LE. Bacteria/plant growth-promotion. Encycl Soils Environ. 2005;1:103-115.
49. Kim DG, Riggs RD. Characteristics and efficacy of a sterile hyphomycete (ARF18), a new biocontrol agent for Heterodera glycines and other nematodes. J Nematol. 1991;23:275.
50. Trivedi P, Spann T, Wang N. Isolation and characterization of beneficial bacteria associated with citrus roots in Florida. Microb Ecol. 2011;62:324-336.
51. Weller DM. Pseudomonas biocontrol agents of soilborne pathogens: Looking back over 30 years. Phytopathology. 2007;97:250-256.
52. Bashan Y. Inoculants of plant growth-promoting bacteria for use in agriculture. Biotechnol Adv. 1998;16:729-770.
53. Scheuerell SJ, Sullivan DM, Mahaffee WF. Suppression of seedling damping-off caused by *Pythium ultimum*, P. irregulare, and *Rhizoctonia solani* in container media amended with a diverse range of Pacific Northwest compost sources. Phytopathology. 2005;95:306-315.
54. Larkin RP, Tavantzis S. Use of a plasmid-cured strain of Pseudomonas fluorescens to evaluate the effect of plasmid pE1 upon efficacy and persistence against *Rhizoctonia solani* in biological control of potato. Biol. Control. 2013;64:313-322.
55. Rosenberg K, Bertaux J, Krome K, Hartmann A, Scheu S, Bonkowski M. Soil amoebae rapidly change bacterial community composition in the rhizosphere of Arabidopsis thaliana. ISME J. 2009;3:675-684.
56. van Diepeningen A, de Vos O, Korthals G, van Bruggen A. Effects of organic versus conventional management on chemical and biological parameters in agricultural soils. Appl. Soil Ecol. 2006;31:120-135.
57. Shoresh M, Yedidia I, Chet I. Involvement of jasmonic acid/ethylene signaling pathway in the systemic resistance induced in cucumber by *Trichoderma asperellum* T203. Phytopathology. 2005;95:76-84.
58. Johnson L, Curl EA, McGovern RJ. Suppression of dollar spot on creeping bentgrass by Rhizobacteria. Plant Dis. 1993;77:288-292.
59. Goswami D, Vaghela H, Parmar S, Dhandhukia P, Thakker J, Dusane D, Vohra R. Pseudomonas oleovorans MSP6 from marine water produces a new rhamnolipid containing a 3-(3-hydroxyalkanoyloxy) alkanoic acid dehydrated moiety. J Appl Microbiol. 2013;115:435-447.
60. Wei Z, Yang X, Yin S, Shen Q, Ran W, Xu Y. Efficacy of Bacillus-fortified organic fertiliser in controlling bacterial wilt of tomato in the field. Appl Soil Ecol. 2011;48:152-159.