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Review

Research Progress on Biocontrol of Pine Wilt Disease by Microorganisms

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Abstract: Pine wilt disease is a malady caused by a complex interaction of various factors such as pine wood nematodes, host plants, vector insects, associated fungi and bacteria, human economic and logistics activities, and environmental factors. The use of microorganisms to biologically control pine wilt disease is a potentially environmentally friendly means for the prevention and control of the disease. In this study, we carried out a systematic review of the progress in research on the biocontrol of pine wilt disease, by focusing on the pathogenic pine wood nematode, its vector beetle, and the host pine tree species. Then, we discuss the implementation prospects and research trends associated with the biocontrol of pine wood disease. This study provides reference information for the understanding and application of various biocontrol microorganisms in the prevention and control of pine wood disease and for the establishment of an environmentally friendly prevention and control strategy.

Keywords: pine wilt disease; biocontrol microorganisms; *Bursaphelenchus xylophilus*; *Monochamus alternatus*; pine

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1. Introduction

Pine wilt disease (PWD) is a complex disease system due to complex host–vector–pathogen interactions and their associated microorganisms, etc. [1–3]. The host trees are usually *Pinus* spp. The pathogen is *Bursaphelenchus xylophilus* (Steiner & Buhrer), i.e., pine wood nematode (PWN) [4], with *Monochamus* spp. [5] as the main vector. The PWN originated from North America and is currently distributed in China, Japan, South Korea, Spain and Portugal, posing a huge threat to global forest ecosystems [3,6]. For example, since the introduction of PWD, the disease has led to high mortality in pine trees in Japan for the past hundred years; forest losses due to the high mortality in pine trees have been more than 50 million m^3 in 10 years from 2004 to 2014 and financial losses due to PWD in Japan have been estimated to be USD 3.7 billion [7]. Since PWD was first reported in Zijinshan, Nanjing, Jiangsu Province, China in 1982 [8], the disease has spread and it is still spreading rapidly in mainland China, becoming the most dangerous and devastating forest disease in China.

Currently, the treatment of PWD is primarily based on physical and chemical prevention and control, such as burning/fumigation of dead wood caused by PWN, and trunk injection of insecticides into diseased trees [9–12]. Although these methods are, to a certain extent, effective, they have a significant negative impact on the environment [7,13]. It has been predicted that by 2030, PWD could spread to over 8%–34% of Europe, and if PWN is not controlled, the cumulative value of lost forestry stock is estimated to reach EURO 22 billion [7]. In recent years, with increasing attention to environmentally friendly control strategies, PWD biocontrol agents have attracted much attention as environmentally safe alternatives for plant protection [14–16]. In this study, we reviewed the current studies

on biocontrol measures targeting PWN, *Monochamus alternatus*, and the host pine trees. The review data were collected from CNKI (China National Knowledge Infrastructure), PubMed, and the Web of Science, from 1980 to 2021.

Physical control is a highly effective control method, such as felling and burning infected pine trees, but it is very expensive, and its use is restricted to periods when the forest fire risk is low. Furthermore, our suggestion is that there should be three PWD management strategies: (i) control the pine nematodes themselves, (ii) control the insect vectors, and (iii) increase the resistance to PWN. Finally, biological control of PWD could be achieved using biocontrol agents (BCAs) of PWN and its BCA vectors (mainly *Monochamus* spp.).

2. Biocontrol of PWN by Microorganisms

In 1982, Yamanaka et al. [17] reported that the culture media of *Phomopsis* sp. had a strong nematicidal activity for PWN, and the fatality rate reached 96.9%–99.6% after treating PWN for 48 h. Since then, additional studies have been conducted on the biocontrol of PWN. Table 1 shows the primary species and strong active strains.

Table 1. Diversity of biocontrol microorganisms and their active substances against PWN.

Strain	Bioactive Substance	Potential Efficiency	Source	Reference
Fungi				
Aspergillus sp.	5-Hydroxymethyl -2-furoic acid	Positive	Soil	Kimura et al. [18]
Fusarium bulbicola	Beauvericin (1)	Positive	Soil	Shimada et al. [19]
Aspergillus fumigatus	Fumiquinones A and B	Positive	Soil	Hayashi et al. [20]
Oidiodendron sp.	4-Hydroxyphenylacetic acid; oidiolactone D	Positive	Soil	Ohtani et al. [21]
Trichoderma sp.	VOCs (volatile organic compounds): 1β-vinylcyclopentane-1α,3α-diol; 6-pentyl-2H-pyran-2-one (2); 4-(2-hydroxyethyl)phenol	Positive	Soil	Yang et al. [22]
Syncephalastrum racemosum Sr18	Culture filtrate (not identified)	Positive	Soil	Hou et al. [23]
Syncephalastrum racemosum Sr18	Fermentation filtrate (not identified)	Positive	Soil	Wang et al. [24]
Annulohypoxylon sp. FPYF3050	VOCs: 1,8-cineole; (+)-sativene; isocaryophyllene	Positive	*Neolitsea pulchella*	Li et al. [25]
Geotrichum sp. AL4	1-[(2R*,4S*,5S*)-2-chloro-4-methyl-1,3-oxazinan-5-yl] ethenone; [2,3-dihydro-2-(1-methylethenyl)-1-benzofuran-5-yl] methanol; and 1-(2,4-dihydroxyphenyl)ethanone	Positive	*Azadirachta indica*	Li et al. [26]
Fusarium oxysporum EF119	Bikaverin, fusaric acid, etc.	Positive	*Capsicum annuum*	Kwon et al. [27]
Xylaria sp. FDYS-1	Culture filtrate (not identified)	Positive	*Quisqualis indica*	Yuan et al. [28]
Penicillium sp. *Colletotrichum* sp. *Phomopsis* sp. *Aspergillus* sp.	Crude methanol extract (not identified)	Positive	*Derris elliptica* *Derris albo* *Derris thyrsiflora*	Sun et al. [29]
Alternaria sp. Samif01	Alternariol 9-methyl ether, etc.	Positive	*Salvia miltiorrhiza*	Lou et al. [30]
Acremonium sp. BH0531	Culture filtrate (not identified)	Positive	Seawater	Meng et al. [31]

Table 1. *Cont.*

Strain	Bioactive Substance	Potential Efficiency	Source	Reference
Verticillium sp. HZ-1-1	Culture filtrate and crushed mycelial filtrate (not identified)	Positive	Seawater	Xu et al. [32]
Penicillium sp. ML-5	Culture filtrate (not identified)	Positive	Seawater	Li et al. [33]
Ophioceras commune *Pseudohalonectria adversaria* *Pseudohalonectria lignicola* *Massarina thalassioidea* *Caryospora callicarpa* *Annulatascus* sp. *Helicomyces roseus* *Phomatospora berkeleyi* *Pseudohalonectria lignicola*	Aliphatic extracts (not identified)	Positive	Freshwater	Dong et al. [34]
Gliocladium roseum YMF1.00133 *Paraniesslia* sp. YMF1.01400 *Pseudohalonectria adversaria* YMF1.01019 *Caryospora carllicarpa* YMF1.01026	Gliocladines A–D; glioclatine; (2S,2′R,3R,3′E,4E,8E)-1-O-(β-D-glucopyranosyl)-3-hydroxyl-2-[N-2′-hydroxyl-3′-eicosadecenoyl]amino-9-methyl-4,8-octadecadiene; 3,5-dihydroxyaldehyde-4-hydroxyl-acetophenone; pseudohalonectrin A and B; caryospomycins A–C	Positive	Freshwater	Dong et al. [35]
Paraniesslia sp. YMF1.01400	(2S,2′R,3R,3′E,4E,8E)-1-O-(β-D-glucopyranosyl)-3-hydroxyl-2-[N-2′-hydroxyl-3′-eicosadecenoyl]amino-9-methyl-4,8-octadecadiene; (2S,2′R,3R,3′E,4E,8E)-1-O-(β-D-glucopyranosyl)-3-hydroxyl-2-[N-2′-hydroxyl-3′-octadecenoyl]amino-9-methyl-4,8-octadecadiene	Positive	Freshwater	Dong et al. [36]
Pseudohalonectria adversaria YMF1.01019	Pseudohalonectrin A and B	Positive	Freshwater	Dong et al. [37]
Caryospora callicarpa YMF1.01026	Caryospomycins A–C	positive	Freshwater	Dong et al. [38]
Camposporium quercicola YMF1.01300 *Periconia digitata* *Caryospora callicarpa* YMF1.0102 *Melanospora zamiae* YMF1.00948	4,8-Dihydroxy-3,4-dihydronaphthalen-1(2*H*)-one; 4,6-dihydroxy-3,4-dihydronaphthalen-1(2*H*)-one; 4,6,8-trihydroxy-3,4-dihydronaphthalen-1(2*H*)-one); 3,4,6,8-tetrahydroxy-3,4-dihydronaphthalen-1(2*H*)-one(cis-4-hydroxyscytalone)	Positive	Freshwater	Zhu et al. [39]

Table 1. *Cont.*

Strain	Bioactive Substance	Potential Efficiency	Source	Reference
Coelomycetes sp. YMFl.01029	Preussomerin C; preussomerin D; preussomerin E; (4RS)4,8-dihydroxy-3,4-dihydronaphth alen-1(2*H*)-one; 4,6,8-trjhydfoxy-3,4-dihydronaphthalen -1(2*H*)-one	Positive	Freshwater	Dong et al. [40], Zhou et al. [41]
Ophioceras dolichostomum YMF1.00988	Ophiocerol	Positive	Freshwater	Dong et al. [42]
Gliocladium roseum YMF1.001331	Gliocladin C and 5-n-heneicosylresorcinol	positive	Freshwater	Song et al. [43]
Arthrobotrys cladodesr A.oligospora A.musiformis A.dendroides Dactylellina elopspora Monacrosporium thaumasium	/	Positive	Nematode-trapping fungus	Zhang et al. [44]
Esteya vermicola ATCC74485 *E. vermicola* CBS115803 *E. vermicola* CNU120806 *E. vermicola* NKF13222	Serine protease	Positive	Endoparasitic microorganism of *Bursaphelenchus xyloppilus*	Liou et al. [45], Kubátová et al. [46], Wang et al. [47], Wang et al. [48], Wang et al. [49]
Arthrobotrys sp.	/	Positive	Nematode-trapping fungus	Saiki et al. [50]
Monacrosporium cystosporium CGMCC1309	Extracellular protease	Positive	Nematode-trapping fungus	Yang et al. [51]
Drechslerella dactyloides cnu091025 *D. dactyloides* cnu091026	/	Positive	Nematode-trapping fungus	Wang et al. [52]
Arthrobotrys dactyloide Dactylaria leptospora Bacteria	/	Positive	Nematode-trapping fungus	Ren and Tang [53]
Pseudoduganella violaceinigra G5-3	VOCs: 2,5-dimethyl pyrazine; 4-dimethylaminopyridine; benzyl acetate; phenethyl butyrate; phenethyl alcohol	Positive	Soil	Wang et al. [54]
Bacillus sp. SMrs28	4-Oxabicyclo[3.2.2]nona-1(7), 5,8-triene; (3S, 8aS)-hexahydro-3methylpyrro[1,2-a]pyrazine-1; 4-dione	Positive	Soil	Zeng et al. [55]
Bacillus thuringiensis 020 and RBT-200701	Parasporal crystal	Positive	Soil	Xu et al. [56]

Table 1. *Cont.*

Strain	Bioactive Substance	Potential Efficiency	Source	Reference
Bacillus simplex *B. subtilis* *B. weihenstephanensis* *Stenotrophomonas maltophilia* *Microbacterium oxydans* *Serratia marcescens*	VOCs: phenol; 2-octanol; benzaldehyde; benzeneacetaldehyde; decanal; 2-nonanone; 2-undecanone; cyclohexene; dimethyl disulfide	Positive	Soil	Gu et al. [57]
B. cereus JK-XZ3 *B. velezensis* HR10 *B. pumilus* YH-20	Fermentation filtrate (not identified)	Positive	Soil	Zhang et al. [58]
Stenotrophomonas maltophilia G2	A novel virulence serine protease	Positive	Soil	Huang et al. [59]
Flectobacillus rhizosphaerae G8-1	Fermentation filtrate (not identified)	Positive	Soil	Wang et al. [60]
B. pumilus LYMC-3	2-{3-[(3S,8aS)-1,4-dioxooctahydropyrrolo [1,2-a] pyrazin-3-yl] propyl}guanidine	Positive	*P. massoniana*	Li et al. [14]
Stenotrophomonas sp. EB394 *Bacillus* sp. EB 93	Ethyl acetate extract (not identified)	Positive	*P. densiflora*	Ponpandian et al. [61]
Brevundimonas diminuta LCB-3	(*R*)-(-)-2-ethylhexan-1-ol	Positive	*Euphorbia pulcherrima*	Zheng et al. [62]
Escherichia coli M131/M132 *Serratia marcescens* M44	Ethyl acetate extract (not identified)	Positive	*Pinus* sp.	Liu et al. [63]
Bacillus amyloliquefaciens JK-JS3	Hexahydro-5-methyl-1-phenyl-1,3,5-triazine-2-thione; 2,2-dimethyl-N-phenylpropanethioamide; [(4,7,7-trimethyl-3-bicyclo[2.2.1]heptany lidene)amino]urea	Positive	*Pinus massoniana*	Zhu et al. [64]
Pseudoalteromonas marina H-42 *Vibrio atlanticus* S-16	VOCs: dimethyl disulfide; benzaldehyde; dimethyl trisulfide; *tert*-butylamine; acetone; dimethylamine, N(diisopropylphosp hino)methyl-	Positive	Seawater	Yu et al. [65]
Bacillus megaterium PX3-1\PX3-2	Culture filtrate (not identified)	Positive	Seawater	Zheng et al. [66]
Pseudoalteromonas nigrigaciens G-23	Culture filtrate (not identified)	Positive	Seawater	Yu et al. [67]
Novosphingobium pokkalii G8-2 Actinomycetes	VOCs: acetophenone	Positive	Freshwater	Wang et al. [54]
Streptomyces sp. AN091965	Spectinabilin	Positive	Soil	Liu et al. [68]
Streptomyces sp. C611	Furaltadone	Positive	Soil	Huang et al. [69]
S. avermitilis AVE-H39	13α-Hydroxymilbemycin β13; 26-methyl-13α-hydroxymilbemycin β13	Positive	Soil	Wang et al. [70]
Amycolatopsis lurida *Nocardia* sp. *Kitasatospora* sp.	Fermentation filtrate (not identified)	Positive	Soil	Xu et al. [71]

Table 1. *Cont.*

Strain	Bioactive Substance	Potential Efficiency	Source	Reference
Streptomyces sp. 680560	Teleocidin B4	Positive	Korean pines	Kang et al. [15]
Streptomyces sp. AE170020	Aureothin; alloaureothin	Positive	Korean pines	Kang et al. [16]
Erwinia sp. A41C3 *Rouxiella* sp. Arv20#4.1	Catecholate-type siderophore; hydroxamate-type siderophore	Positive	*Pinus pinaster*	Proença et al. [72]
Streptomyces sp. HA07011	Fermentation filtrate (not identified)	Positive	Seawater	Lei et al. [73]
Kocuria sp. HT-11	Culture filtrate (not identified)	Positive	Seawater	Chen et al. [74]
Streptomyces termitum HT-8	Culture filtrate (not identified)	Positive	Seawater	Chen et al. [75]

2.1. Diversity of Active Biocontrol Strains

As shown in Table 1, PWN biocontrol microorganisms mainly come from soil, plant endophytes, freshwater, ocean water, PWN endoparasites, and predatory microorganisms, and can be divided into fungi, bacteria, and actinomycete microorganisms. There are a total of 51 genera, 51 species, and nearly 100 strains. Among them, fungi are the most prevalent, including 33 genera, 27 species, and 53 strains, such as *Arthrobotrys* [44], *Aspergillus* [18], *Esteya* [76], *Fusarium* [19], *Massarina* [34], and *Pseudohalonectria* [35]. Bacteria come in second in quantities, including 13 genera, 21 species, and 28 strains, such as *Bacillus* [61], *Stenotrophomonas* [61], *Pseudoduganella* [54], *Brevundimonas* [62], *Vibrio* [65], etc. Among these, *Bacillus* is the prevailing genus. There are currently only a few studies on PWN biocontrol using actinomycetes that have mainly included 5 genera (*Amycolatopsis*, *Kitasatospora*, *Kocuria*, *Nocardia*, and *Streptomyces*), 3 species, and 11 strains. In addition to the above sources, active strains have been isolated and obtained from saprophyte [25,77], edible fungi [78–81], and PWN body surfaces [82–84]. Hao et al. [85] even isolated a strain of *Bacillus* sp. with strong PWN nematicidal activity from the surface of pickled mustard.

2.2. Nematicidal Substances from Active Microorganisms

There are a total of 76 active substances from biocontrol microorganisms that work against PWNs, including polyketones, lipopeptides, quinones, alkaloids, piperazines, phenols, terpenes, aldehydes, siderophores, and furans, with overall lethality rates ranging from 4 to 100%. Among them, there are 26 volatile organic compounds (VOCs) (Table 1). There are 37 fungi-derived active substances, such as fumiquinones A and B [20], beauvericin (1) [19], and oidiolactone D [22], all of which have demonstrated excellent biocontrol efficiency. As of 2021, there were only two published studies on fungal VOCs killing PWN. Yang et al. [22] reported the nematicidal activity of three fungal VOCs against PWN for the first time. Li et al. [86] reported the nematicidal activity of VOCs from the plant endophyte *Annulohypoxylon* sp. FPYF3050, the lethality rates for second-stage juveniles (J2) and mixed-stage juveniles were 64.1% and 58.4%, respectively, and the main component of VOCs was 1,8-cineole. Moreover, there have been 32 active substances derived from bacteria, such as 4-oxabicyclo[3.2.2]nona-1(7), 5,8-triene [55] and parasporin crystallin derived from *Bacillus*, all of which have shown strong nematicidal activities [56]. There have been numerous studies on bacterial VOCs against PWN, involving more than 20 bacteria. For example, Gu et al. [57] obtained a variety of VOCs such as phenol, 2-octanol, and benzaldehyde, whose lethality rate reached 80%–100%. Yu et al. [65] reported, for the first time, the nematicidal activity of marine microbial VOCs, such as dimethyl disulfide and benzaldehyde. There are primarily seven active substances derived from actinomycetes that have shown strong nematicidal activity, such as teleocidinb4, aureothin, and alloaureothin derived from the plant endophyte *Streptomyces* sp. In pot seedling experiments,

aureothin and alloaureothin effectively inhibited the occurrence of PWD in 4-year-old red pine plants [15,16].

In summary, existing studies on PWN biocontrol microorganisms have mainly focused on the screening and identification of nematicidal active strains, and the isolation and identification of active substances. A total of almost 100 active strains and 76 active substances have been reported. However, in most studies, no further analysis was carried out on the active strains or their active substances. In addition, there have been a few studies on the nematicidal activity and physicochemical properties of active strain culture filtrate and crude extract and the optimization of the cultivation conditions of the nematicide active substances [23,34,58,61,63,68]. Although such studies did not carry out isolation and identification of active substances or further research, they still provided rich microbial resources for the prevention and control of PWD. It should be noted that a series of systematic studies have been performed on the parasitic fungus *Esteya vermicola* [87–93]. These studies examined its attraction to PWN and explored the development, transportation, preservation, colonization, and parasitic modes of conidia preparations [87–93], and provided information on the practical application of active strains.

In view of PWN taxonomy, ecology, disease cycle, and epidemiology [4,7,94,95], the infection, damage, and invasion of PWN represent a complex interaction of various factors. However, the most critical mechanisms of tree death, i.e., how such tiny nematodes kill such massive pine trees so rapidly, is still not clear. Ultimate strategies to manage this disease should be developed based on the mechanisms of tree death.

3. Biocontrol of *Monochamus* by Microorganisms

Monochamus alternatus (pine sawyer beetle) is the main stem-boring pest of pine plants such as *P. massoniana*, *P. thunbergii*, and *P. densiflora*, and its adults are the main vectors of PWN and play a key role in the spread of PWD [96]. With *M. alternatus* as the target species, breaking the infection cycle of PWN is one of the keys to the comprehensive control of PWD. Research in this area has mainly centered on the entomopathogenic fungi *Beauveria* and *Metarhizium*. The main active strains and active substances are shown in Table 2.

3.1. Diversity of Beauveria and Metarhizium

The studies of *Beauveria* have predominantly focused on *B. bassiana* and *B. brongniartii*. There is a total of 16 active strains that have been reported for the vector beetle biocontrol, including *B. bassiana* F-263 [97,98], *B. brongniartii* F-877, and *B. brongniartii* #879 [97]. The fatality rate of *Monochamus alternatus* in laboratory conditions has been reported to be in the range of 43%–100%. As for *Metarhizium*, there are three species: *Metarhizium anisopliae*, *M. pemphogum*, and *M. pingshaense*, a total of 16 strains (as shown in Table 2). Under laboratory conditions, the fatality rate of *Monochamus alternatus* has been reported to be in the range of 37%–100%. *Metarhizium anisopliae* was the main researched species in the published studies.

Table 2. Biocontrol microorganisms in the control of *Monochamus alternatus*.

Strain	Bioactive Substance	Source	Reference
Beauveria brongniartii #879 *B. brongniartii* F-877 *B. bassiana* F-263	Not identified	*Psacothea hilaris* and *Monochamus alternatus*	Shimazu, [97]
B. bassiana F-263	Not identified	*M. alternatus*	Maehara et al. [98]
B. bassiana B36	Protein toxin	*Dendrolimus punctatus*	Li et al. [99]
B. bassiana B7/B9	Not identified	*M. alternatus*	He et al. [100]
B. bassiana B1-B8	Not identified	*M. alternatus*, *D. punctatus* and *Anoplophora glabripennis*	Sun et al. [101]
B. bassiana B252/B305	Not identified	*M. alternatus*	Wang et al. [102]
B. bassiana sp.	Protein toxin	Not mentioned	Mei et al. [103]
M. anisopliae JEF-279	Destruxin and protease	Soil	Kim et al. [104]

Table 2. *Cont.*

Strain	Bioactive Substance	Source	Reference
M. anisopliae JEF-197 *M. anisopliae* JEF-271 *M. anisopliae* JEF-279	Not identified	Soil	Kim et al. [105] Kim et al. [106]
M. pingshaense WP08 *M. pingshaense* WTKH *M. anisopliae* LV2 *M. pemphogum* qc1401	Not identified	*Brontispa longissima*, *Melanotus cribricollis*, and *Popillia* sp.	Zhang et al. [107]
Metarhizium anisopliae Ma83	Not identified	*Saperda populnea*	Wang et al. [108]
M. anisopliae 1291 *M. anisopliae* 1349 *M. anisopliae* 2049	Not identified	*M. alternatus* and cydnid bug	He et al. [109]
M. anisopliae MaYTTR-03 *M. anisopliae* MaYTTR-04	Not identified	Soil	He et al. [110]
M. anisopliae MaYTTR-04	Not identified	Soil	He et al. [111] He et al. [112] Cai et al. [113]
M. anisopliae var. *anisopliae*	Not identified	Not mentioned	Ma et al. [114]
M. anisopliae Ma_{789}	Not identified	Not mentioned	Pan et al. [115] Pan et al. [116]
M. anisopliae var. *major* CQMa117	Not identified	*M. alternatus*	Yin et al. [117]
Bacillus thuringiensis Cry3Aa	Coleopteran-specific Cry3Aa toxin	\	Guo et al. [118] Guo et al. [119]

3.2. Active Ingredients

There are currently few studies on metabolites that can directly kill or accelerate the death of *Monochamus alternatus* from the perspective of the metabolism of entomopathogenic fungi. The existing studies have mainly focused on toxic protein and destruxins. For example, 12 types of single protein extracts were isolated from the whole protein extract of *Beauveria bassiana*, which showed strong injection toxicity to the larvae of *Monochamus alternatus*, resulting in food refusal, slow movement, and rapid death [99]. Kim et al. [104] studied the simultaneous saccharification culture protocol where *M. anisopliae* JEF-279 efficiently produced destruxins, and the *Monochamus alternatus* were treated with a mixture of destruxins and protease-containing culture filtrate for 5 days, and the fatality rate was 100%.

To recapitulate, the research on biocontrol microorganisms used to control *Monochamus alternatus* has principally involved the selection of entomopathogenic fungal strains and the isolation and identification of active substances. A total of five species of *Beauveria bassiana* and *Metarhizium anisopliae* and 32 strains have been identified and utilized. The active substances are mainly protein toxins and destruxins. Based on existing research, two entomopathogenic fungi are mainly involved in the prevention and control of *Monochamus alternatus* in the form of conidia [97,100–102,105–117]. For instance, the conidia of *M. anisopliae* JEF-197, 271, and 279 resulted in a 40%–70% fatality rate [105], and the 12-day cumulative corrected mortality rate of *Monochamus alternatus* treated with conidia suspensions of *B. bassiana* B7 and B9 reached 50 ± 10% and 100%, respectively [100]. During the attempted application of entomopathogenic fungi to the field production based on these studies, it was found that the microbial application method was essential for the conidia to contact and infect *Monochamus alternatus*. In addition to conventional spraying and soil application [106], there are mainly three methods of microbial application: wheat bran granule, insect carrier, and non-woven fabric strips. In the wheat-bran pellets method, entomopathogenic fungi are cultured on wheat-bran pellets and implanted under the bark of PWD infected pine trees [120]. The fatality rate of *Monochamus alternatus* on standing trees reached 43%–45% [120]. The insect carrier approach is to convey conidia of entomopathogenic fungi with insects that are likely to interact with *Monochamus alternatus*, and therefore, to achieve effective contact between the conidia and *Monochamus alternatus*. For example, *Cryphalus fulvus* and *Sclerodermus guani* carrying conidia of entomopathogenic fungi resulted in the highest fatality rate of 94.4% in a laboratory environment, and 40.8%

in forest settings [115,121,122]. In the non-woven fabric strips method [123], fabric strips infused with a certain amount of conidia of entomopathogenic fungi are placed on the pine branches. Approximately 80% on average and a maximum of 100% of the larvae were infected and killed with the fungus using this method [123]. A series of studies have evaluated the application potential of the infused non-woven fabric strips method in the field and have improved the details of the method [107,124–126], such as varying the conidia concentration levels and application timing. Such explorations of methodologies have evolved into making this technique the most convenient and effective method for the application of entomopathogenic fungi. However, this process is very labor intensive when applied on a large scale and is even impossible in some mountainous areas.

Indeed, there are many studies on natural enemy insects for biocontrol of *Monochamus alternatus*, and the results have shown that the method can be effective [127,128], however this paper focuses on microorganisms (fungi, bacteria, and actinomycetes), the natural enemy insects are not mentioned.

4. Microorganisms Biocontrol for Improving Pine Resistance and Treating Stumps of Dead Wood Caused by PWN

In 1998, Amano applied the mycelium of *Aspergillus melleus* to the root system of pine trees [129]; two years after inoculation with PWN, 98% of the pine trees survived as compared with 90% for the control group of untreated pine trees [129]. Then, additional studies were carried out to improve the resistance and survival rate of pine trees against PWD utilizing the microorganisms' growth promoting effect and induction of resistance of pine trees [130–135], and other studies focused on treating stumps of dead wood caused by PWN by wood-rotting fungi [136,137]. The main biocontrol microbial groups targeting pine trees are shown in Table 3.

Table 3. Biocontrol microorganisms targeting pine trees.

Strain	Bioactive Substance	Function	Reference
Amanita vaginata *Cladosporium cladosporioides* *Gaeumannomyces cylindrosporus* *Paraphoma chrysanthemicola* *Phialophora mustea* *Suillus laricinus*	Mycelium suspension (not identified)	Growth promotion	Chu et al. [138]
diazotrophic bacteria *Cunninghamella elegans*	Biofertilizer (not identified)	Growth promotion	da Silva et al. [139]
Pseudomonas putida UW4	1-Aminocyclopropane-1-carboxylate (ACC)	Growth promotion	Nascimento et al. [140]
Bacillus thuringiensis JCK-1233	Cyclo-(L-Pro-L-Ile)	Induced resistance	Park et al. [130]
Botrytis cinerea	Not identified	Induced resistance	Takeuchi et al. [131]
Pseudomonas putida 16YSM-E48 *Curtobacterium pusillum* 16YSM-P180 *Stenotrophomonas rhizophila* 16YSMP39	Gamma-aminobutyric acid (GABA)	Induced resistance	Kim et al. [132]
Esteya vermicola CNU 120806	Not identified	Induced resistance	Wang et al. [133] Wang et al. [134] Wang et al. [135]

Table 3. *Cont.*

Strain	Bioactive Substance	Function	Reference
Tremellodon gelatinosum *Fomitopsis pinicola* *Pleurotus ostreatus* *Laetiporus sulphureus* *Poria cocos*	Not identified	Decomposing the stumps of PWD-killed *Pinus* sp. and killing PWN	Deng et al. [136]
Ceriporia sp. J5-2	Not identified	Decomposing the stumps of PWD-killed *Pinus* sp. and killing PWN	Wang et al. [137]

4.1. Active Strain Diversity

The biocontrol microbial groups for targeting the host pine trees have mainly included fungi and bacteria, with a total of 19 genera, 19 species, and 20 strains. Specifically, studies on fungi included 15 genera and 15 strains, such as *Amanita*, *Cunninghamella*, *Esteya*, and *Tremellodon* [133,136,138,139]. The bacteria studied have mainly belonged to four genera and five strains, i.e., *Bacillus thuringiensis* JCK-1233, *Curtobacterium pusillum* 16YSM-P180, *Pseudomonas putida* UW4, *Pseudomonas putida* 16YSM-E48, and *Stenotrophomonas rhizophila* 16YSMP39 [130,132,140].

4.2. Active Substances

From the currently published progressive research, there are few studies on the key active substances of biocontrol microorganisms targeting pine trees; the existing studies have mainly included ACC, GABA, and cyclo-(L-Pro-L-Ile) [130,132,140]. For example, by treating pine seedlings with ACC-producing *Pseudomonas putida* and its mutants, it has been found that the wild strain accelerated the crown development of pine seedlings and reduced the symptoms of PWD as compared with the mutants [140]. This was the first study on the application of ACC deaminase-producing bacteria as a potential biocontrol agent for forest diseases. In addition, it has been confirmed that *Bacillus thuringiensis*-derived cyclo-(L-Pro-L-Ile) could moderately enhance the expressions of *P. densiflora* pathogenesis-related genes *PR-1, PR-2, PR-3, PR-4, PR-5*, and *PR-9* and mitigate the outbreak of hypersensitive reactions in pine seedlings [130]. The active substances related to wood-rotting fungi in the treatment of PWN-infected dead wood stumps have not yet been reported.

To summarize, biocontrol microorganisms can target pine trees and have been shown to have the ability to promote growth, induce resistance, and treat dead wood stumps caused by PWN. The research on active substances is relatively scarce, having mainly been focused on ACC, GABA and cyclo-(L-Pro-L-Ile). Most of the studies have been carried out utilizing microbial cells [131,133–139]. In terms of arboreal growth promotion, biocontrol microorganisms can reduce the severity and development of PWD by alleviating the typical symptoms of diseased trees, such as weakened photosynthesis, reduced water conduction, and transpiration disturbances [141]. For instance, a biofertilizer rich in diazotrophic bacteria and chitosan-producing fungi can reduce the number of PWNs in pine trees by 36.3 times, while inhibiting the decline of photosynthetic pigments and water content and significantly increasing the biosynthesis of soluble polyphenolics and malondialdehyde in pine trees, thereby enhancing the resistance of pine trees to PWN [139]. In terms of induction of infection resistance, biocontrol microorganisms can induce a PWD defense response in pine trees. For instance, pre-inoculation with *Botrytis cinerea* delayed the development of symptoms caused by PWN, and the fatality rate was reduced by 10% [131]. Growth promotion and induction of resistance of pine trees to PWD are both initiated due to the interaction between biocontrol microorganisms and pine trees physiology. In addition, dead wood stumps contain PWN and larvae of *Monochamus alternatus*, which are one of the important sources of PWD infection and increase the difficulty of eradicating PWD [136,137]. The most common treatment methods currently include tree stump burning and chemical

fumigation, which have significant negative impacts on the environment. In scientific research, it has been reported that wood-rotting fungi could be used to treat dead wood stumps, and several strains with strong colonization ability, decomposition ability, and nematicide activity have been screened [136,137]. Thus, there have been effective attempts to pursue environmentally friendly and effective treatments of dead wood stumps, and also the accumulation of fungi strain resources that can be utilized.

5. Potential Prospects

Due to significant ecological and economic losses caused by PWD in natural coniferous forests, many scientists have tried numerous methods to manage PWD. Physical and chemical controls are highly effective, including felling, crushing, and burning infected pine trees or trunk-injection agents, which are both major strategies for eradication and have been used for prevention [7]. However, physical control is expensive because it requires intensive labor, increases forest fire risk, and pollutes the environment. Chemical agents have been recently recognized as causing environmental pollution and bioaccumulation, and their use has decreased [7,142]. Demand for alternative control agents or biological controls with low or no environmental risks has been increasing; this are clear advantages to develop BCAs as microorganisms (fungi, bacteria, and actinomycetes), and research on them should be actively conducted. Nowadays, most of experiments have primarily been conducted in controlled environments; however, there are many factors that affect the application of biocontrol microorganisms into forests. Researchers have identified several ideas which have the potential to solve these factors and provide new directions for managing PWD in the future.

5.1. Endophytes

Colonization in pine trees is one of the keys to the application of biocontrol microorganisms in forests. Plant endophytes are derived from pine trees or other plants, they are more likely to be colonized in pine trees than biocontrol microorganisms from other sources. In addition, endophytes have co-evolved with these hosts for a long time, and they can produce the same or similar active substances as their hosts. Therefore, clearly it is more effective to isolate and screen biocontrol bacteria from plants that produce active substances against PWN [143]. Despite all this, the use of endophytes has been limited to controlled environments, and therefore, further applications are needed. As compared with physical and chemical methods, the application of endophytes in forests needs to improve colonization rate, efficiency, stability, and specialization, and therefore, the method could play a sustainable role. Perhaps, the knowledge of plant microbiomes could provide a new way to improve the use of plant endophytes to control diseases and pests. For example, Tian et al. [144] determined the key endophytes from the core communities of the tomato root microbiome and assessed the potential of the function that protected the host from pathogens at the community.

5.2. Entomopathogenic Fungi

Fugal entomopathogens have been proposed as environmentally friendly alternatives to chemical control [145]. PWN is mainly carried and spread by the insect vector *Monochamus alternatus*. Therefore, if *M. alternatus* is controlled, PWD can be indirectly controlled [146]. Current research is mostly on the larvae of *M. alternatus*. However, during the infection cycle of PWD, the adult stage of *M. alternatus* is the only time when the insect and pathogenic nematodes are exposed outside the bark of trees. Hence, targeting the adults with a wide distribution, as well as the screening and cultivation of excellent entomopathogenic fungal strains with strong pathogenicity are significant strategies for effective applications. The effectiveness of entomopathogenic fungi are limited by their susceptibility to ultraviolet light and low moisture [145]. As many entomopathogenic fungi are endophytes, for example, *Metarhizium*, the use of fungal entomopathogens as endophytes might provide a novel alternative for overcoming the above obstacles. In

addition, a deeper understanding of the interaction mechanisms among entomopathogens and their hosts in the ecology of pine forests could provide correct guidance for making this technology an effective alternative to chemical control.

5.3. VOCs

VOCs are an important class of natural metabolites with the characteristics of strong diffusivity and long-distance transmission, which make them exert their inhibitory activity without requiring a direct or physical contact between the VOCs-producing microorganism and the target pathogen [147,148]. VOCs from BCAs have resulted in being highly effective even at low concentrations with reduced release of residual and negligible hazardous effects on the animals and the environment [149]. In addition to pathogen inhibition [150], microbial VOCs have also been shown to be involved in a wide variety of processes, such as killing plant-parasitic nematodes [151], promoting plant growth [152], and promoting induction of resistance mechanisms [153]. Nevertheless, research on the activity of single components of VOCs is generally missing in field studies. Studies that have been carried out in vitro and/or greenhouse conditions have generally succeeded in the evaluation of the biological mechanisms triggered by the microbial VOCs but have not considered the practicability under open-field conditions [149]. The existing VOC nematicidal studies have mainly focused on the nematicidal activity of plant-derived VOCs and the nematicidal activity of microbial VOCs against *Meloidogyne* [154,155]. The study of nematicidal activity of microbial VOCs targeting PWN is a new direction and still in its infancy. Since breakthroughs are urgently needed in the prevention and control of PWD, microbial VOCs may be a worthwhile direction for future in-depth research.

5.4. Synthetic Biology

The instability and low yields of active substances is one of the factors that restrict their application in forests. Within the core of "artificial design and genome editing", synthetic biology conceives of expression elements or modules from an engineering point of view and can be used to produce specific target products. With the development of science and technology, additional research fields have become involved in the prevention and control of PWD, such as molecular biology [156]. On the one hand, techniques such as cloning and gene knockout have been used to explore the role of key active substances and their encoded genes such as external alkaline proteases BLG4 [157], *purl* [158], and Cry protein [118,119] from biocontrol microorganisms in treating PWN and *Monochamus alternatus*. On the other hand, by combining with molecular biology techniques, the physicochemical properties of active substances can be improved, and new active substances have been obtained, such as avermectin B1a glycosides [159], *O*-glycosides [160], tenvermectin A and B [161] and violacein 5′-*O*-diglucoside [162]. These studies have provided theoretical references and basic substrates for breaking the strain limitation and artificially synthesizing specific and stable PWN active substances with high production. Although such technology is in the medium- to long-term future, the development of this type of technology will not be beyond criticism, and many of the societal issues that confront the development of genetically modified crops will also need to be addressed regarding designer biological control agents. Nevertheless, in the long term, in the epoch of synthetic biology, new combinations of functional traits can be assembled in novel systems that, so far, have been unimaginable [163].

5.5. Induced Resistance

PWD is difficult to cure once it occurs [164]; therefore, enhancing pine resistance is an effective preventive measure. Induced resistance (IR) is the stress response of plants under the influence of external factors, which is common in *Pinus*, and not specific to a particular host species [165]. Fungi and bacteria have exhibited inducted resistance in pine trees, such as *Botrytis cinerea* (avirulent) and *Bacillus thuringiensis*. It has been reported that pine endophytes may play a role in the induction of resistance through

bacterially produced siderophores and lipases [166,167]. In addition, analyses of the pine microbiome have revealed homologous sequences to traits associated with plant growth-promoting and plant defense factors (e.g., chitinases). The rich microbial communities of pine trees represent functional resources that are untapped and have the potential to be applied to achieve environmentally friendly prevention and control stratagems towards this devastating disease [168]. However, tree protection strategies based on IR are in the early stages and there are many challenges to be overcome. For example, characterization of the endogenous signaling pathway, which is the most critical step to the development of IR for trees [169]; the trade-off between disease resistance and the high costs of activating defenses involved in IR [170]; environmental factors that will influence the efficacy and effectiveness of the IR responses, such as nutrient supply, water availability, and temperature [169]. Clearly, these will need to be addressed if we are to develop and exploit IR as an alternative, eco-friendly solution for mitigating pest impacts in trees.

5.6. Microbiome

A microbiome is defined as a characteristic microbial community occupying a reasonable well-defined habitat which has distinct physio-chemical properties [171]. Next-generation sequencing (NGS), single molecule real-time (SMRT) sequencing, and RNA-SEQ in microbiome research, combined with traditional plate culture technology, can help scientists grasp a full view of a microbiome and obtain more realistic classification and functions of plant microbial communities, and thus, deeply reveal the relationships among plant microbiomes and plant diseases, and their interactions with pathogens or BCAs. A credible interaction model of a biocontrol system has been established to provide a new method for biocontrol [172,173]. This type of research could provide new ideas about the interaction system of PWN, *Pinus* sp., and microorganisms. For example, much work has been done to understand the mechanism(s) by which such tiny nematodes kill such massive pine trees so rapidly [95], however, there are only some hypotheses on the mechanism of tree death [174,175]. There are significant changes in immune regulation and water physiology during the process from infection of PWN to *Pinus* sp. wilting [176,177]; exploring the roles of biocontrol microorganisms in the above mentioned microbiome process may become a breakthrough to understand the mechanism and to manage PWD.

In general, biocontrol of PWD by microorganisms is a potentially environmentally friendly means, however it cannot replace physical and chemical control in the prevention and control of this disease now. It will be necessary to use a combination of biological, physical and chemical controls in order to achieve rapid control.

6. Conclusions

In general, in laboratory and other small-scale experiments, biocontrol microorganisms have a significant effect on the prevention and control of the above mentioned three components of the PWD disease system. However, PWD is a complex disease system, and therefore, the efficacy of biocontrol measures is affected by such complexity in the field. Moreover, the application of the above methods in forests is comprehensively constrained by logistical, environmental, and climate factors; therefore, there have been few large-scale applications in wild forests. Although a large amount of labor, materials, and financial resources have been invested in the prevention of the disease, which have yielded substantial results, breakthroughs are still needed in the prevention and control of PWD. In this study, we reviewed the progress in research on microorganism-based biocontrol of the three main components of the PWD disease system, namely, PWN, *Monochamus alternatus*, and pine trees. Regarding the studied microorganisms, a total of 69 genera, 72 species, and nearly 150 strains have been involved, including fungi, bacteria, and actinomycetes. The primary isolated sources included the soil and endophyte, marine, freshwater, and endoparasitic fungi of PWN. The ascertained studies mainly focused on the screening and identification of active strains, isolation and identification of active substances, growth promotion and induction of resistance in host pine trees, and treatment of dead wood

stumps affected by PWN. For the next step, according to the characteristics of PWD, new technologies such as synthetic biology should be used to explore stable bacterial species resources and application methods that could be adopted in infected forests, as well as active substances with strong activity, strong resistance to stress, good permeability, and good adhesion, for the purpose of applying the outstanding strains and active substances obtained in laboratory or greenhouse experiments to the field.

In addition, in recent years, the host plants and vector insects of PWD have been constantly changing. The number of pine tree species that can be infected by PWD has reached 60, which is almost all pine plants [178]. It has been confirmed that *M. saltuarius* is an effective transmission medium of PWN [179], and the prevention and control of PWN is becoming more and more imperative. Research on new vector and newly discovered hosts of PWN may become an innovative research direction in the future, which can potentially be used as a supplement to current PWD prevention and control measures. Researchers have contributed important information, as described in Sections 5.1–5.6, aimed at providing a theoretical basis for further research and practical applications of biocontrol microorganisms in the prevention and control of PWD.

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