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Biocontrol of wood-rotting fungi

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Fungal decay and deterioration of softwood and hardwood trees are the most common and damaging problems of forest and timber industries worldwide. A range of microbial as well as insect deteriogens can attack wood. Although some wood types contain chemical extractives that confer resistance against wood decay fungi, most are non-durable and subject to attack by a wide range of fungi, thereby necessitating a broad spectrum controlling action. The wood preserving industry uses chemical wood preservatives that pose adverse health and environmental effects. To avoid this, new biological and biochemical control systems are needed for the preservation of wood decay. This review summarizes the state of art in research and prospective use of wood and rhizosphere-inhabiting actinomycetes as biocontrol agents for brown- and white-rot fungi.

Keywords: biocontrol agents, wood-rotting fungi, antibiosis, mycoparasitism, *Streptomyces violaceusniger*, chitinase
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Introduction

Forests cover about 3870 m ha of land, which accounts to 30% of earth. India with a forest area of 76.5 m ha is one of the largest producers of forest products, worth INR 30,000 crores per annum[1,2]. Wood, the major forest product, is used for variety of purposes, such as building construction, composite manufacture, pulp and paper products, and a variety of finished materials including furniture, ports, pilings and distribution poles. It has been established that wood-rotting fungi, particularly basidiomycetes, damage forest wood even more than insects, marine animals or bacteria[3]. These basidiomycetes are categorized as either white- or brown-rot fungi. Brown-rot fungi (BRF) decompose primarily the carbohydrate component of the wood. Their preferential decomposition of carbohydrate, cellulose and hemicellulose leads to fractures across the grains that break the wood into brown-coloured cubes. There is strong evidence to suggest that involvement of phenol-oxidizing enzymes during brown rot leads to generation of phenoxy radicals [3].

White-rot fungi (WRF), on the other hand, degrade both cellulose and lignin by secretion of cellulolytic and lignolytic enzymes. They decompose lignin of middle lamella sufficiently to cause separation of cells into fibers. The lignin is mineralized via extracellular fragmentation of the lignin polymer into lower molecular weight moieties that are then metabolized intracellularly. Over 600 species of WRF have been found to be lignolytic, converting lignin to carbon dioxide. *Phanerochaete chrysosporium*, a WRF, under nitrogen-limiting condition secretes at least six extracellular lignin peroxidase (LiP) and four manganese-dependent peroxidase (MnP) isozymes[4,5]. Several other WRF secrete unique combinations of peroxidases and oxidases.

Trametes versicolor and *Phlebia radiata* produce one or more laccases in addition to LiP and MnP[6]. *Pleurotus sajor-caju* secretes an aryl alcohol oxidase, a laccase and several peroxidases[7]. *Bjerkandera adusta* secretes an aryl alcohol oxidase, while *Rigidoporous lignosus* and *Dichomitus squalens* (*Polyporous anceps*) secrete a laccase and MnP. MnP has also been implicated in the degradation of wood by the basidiomycete *Neolentinus edodes* [8-11].

Until recently, the wood preserving industry has used three major preservatives, namely creosotes, pentachlorophenol and copper-chrome arsenate. These are broad-spectrum preservatives but pose problems of environmental pollution from the disposal of toxic wastes and health hazard to workers. The immunological consequences of wood workers exposed to pentachlorophenol are reported to be activated T-cells, autoimmunity, functional immunosuppression and B-cell dysregulation[12,13].

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Besides adverse health and environmental effects, legislative constraints to these chemical preservatives suggest the need for new biological and biochemical control systems for preservation of wood.

Mechanism of Biocontrol

Antibiosis and mycoparasitism, the two direct mechanisms of antagonism, have been proposed to explain the inhibition of fungal pathogens in the rhizosphere by biocontrol agents. Antibiosis occurs when one or more diffusible compounds inhibit growth or developmental changes in the pathogen, impairing its ability to colonize the rhizosphere and establish disease. Mycoparasitism, on the other hand, is a different process initiated by physical destruction of fungal cell wall mediated by the action of hydrolytic enzymes produced by the biocontrol agent. A third mechanism, involving competition for space and nutrients within the rhizosphere, has also been of significance.

Evidences for the role of competition and parasitism in the biocontrol of plant diseases have been convincing. However, antibiosis is much less clearly established due to the lack of methods for a meaningful evaluation of the production and function of antibiotics in soil. Fungal cell wall degrading enzymes produced by an antagonist are, therefore, thought to be involved simultaneously in parasitism and antibiosis. Antibiosis, nevertheless, is an advantageous mechanism particularly for biological control of diseases, because compounds mediating antibiosis can diffuse rapidly in nature and direct contact between the antagonist and pathogen is not necessary[14].

Many antibiotics produced by actinomycetes have been used directly, or assumed to be responsible, for the biocontrol activity of the producing strain. Such metabolites may include macrolide, benzoquinones, aminoglycosides, polyenes and nucleoside antibiotics. Certain species of actinomycetes, such as *Streptomyces*, are known to produce not only antibiotics but also extracellular enzymes active in fungal cell wall degradation, such as β-1,3-glucanases and chitinases[15]. The role of these enzymes in antifungal activity and biocontrol is of interest to several research groups[14-17]. Recently, the authors have shown that *Streptomyces violaceusniger* strain XL-2 exhibits strong antagonism towards white- and brown-rot fungi, *Postia placenta, Phanerochaete chrysosporium, Trametes versicolor* and *Gloeophyllum trabeum*[16]. The antagonism is ascribed to the extracellular production of a protein, which is yet to be characterized, though it has the potential to be exploited commercially in healthcare and agriculture industry.

During the last decade, chitinases have received increased attention because of their wide range of applications. Chitin is found in the cuticle of insects and the shells of crustaceans and mollusks. Also, the cell walls of most taxonomic groups of fungi contain chitin. Since the fungal cell walls are rich in chitin, the potential application of chitinase in biocontrol of fungal phytopathogens is promising. Chitinase producing microbial strains might be used directly in biological control of fungi, or indirectly by using purified protein or through gene manipulation[17].

Tree-derived Phenolic Compounds as Control Agents for Wood-decaying Basidiomycetes

Naturally occurring phenolic compounds were used as possible regulators of fungal growth. Taylor *et al*[18] reported that the growth of *Trametes versicolor* on wood was affected in a bimodal fashion via time-dependent application of catechol. Data from other studies also indicated that phenolic compounds (quinones) might regulate hyphal growth in a bimodal fashion through the products of extracellular polyphenol oxidase[19].

The effect of 12 monomeric aromatic compounds on the production of six carbohydrate-degrading enzymes from two BRF, *Postia (Oligoporous) placenta* and *Gloeophyllum trabeum*, and one WRF, *Trametes versicolor* was reported by Highley and Micales[20]. Most compounds at a concentration of 0.05% (w/v) were inhibitory to the growth of the decay fungi. When incorporated into the liquid growth medium of the fungi, some of these compounds inhibited the production of enzymes. Catechol and vanillin (50 ppm) caused complete inhibition of xylanase and β-1,4-endoglucanase production by *P. placenta*. No aromatic monomer, however, strongly inhibited all enzyme activities of all of the fungi. Interestingly, the efficacy of phenolic fraction of the *Hopea parviflora* heartwood and Cashew nut shell liquid was investigated against termites and fungi by Sharma *et al*[21,22]. They found the results encouraging; however, further examination for the efficacy of phenolic compounds as fungal growth control agents is required.

Microfungi as Biocontrol Agents

Much research has centred on the use of *Trichoderma* species as potential control agents for a

wide range of plant pathogens [23-27]. *Trichoderma* spp. are known for rapid colonization of wood, production of lytic enzymes including chitinase and β-1,3-glucanase, and the secretion of volatile and non-volatile fungicidal and fungistatic secondary metabolites[28].

A commercially available mixture of *Trichoderma polysporum* and *T. harzianum* (Binab) was used by Morrell and Sexton [29] to control decay of loblolly pine sapwood and Douglas-fir heartwood by five basidiomycete fungi. Although they achieved good biocontrol against *Neolentinus lepideus* and other BRF when wood was out of ground contact, most of the test fungi were not completely inhibited. The biocontrol agent had little effect on WRF, or even on *N. lepideus*, when wood was exposed to soil. According to the authors, Binab did not appear to be a feasible method for controlling decay of Douglas fir or southern pine poles.

Bruce and Highley[30] tested fifteen isolates of *Trichoderma*, two of *Penicillum*, and one of *Aspergillus* as biocontrol agents against two basidiomycetes, *Trametes versicolor* and *Neolentinus (Lentinus) lepideus*. Although the filtrates for most isolates produced some growth inhibition, only three of the isolates (two *Trichoderma* and one *Aspergillus*) produced sufficient effects against sixteen brown- and white-rot basidiomycetes. The culture filtrates of all three isolates showed varying degrees of inhibition against each of the basidiomycetes; filtrates of the *Aspergillus* producing the best inhibition against WRF. In another study, Bruce *et al*[31] reported that distribution pole interiors colonized by *Trichoderma* were able to resist decay by *N. lepideus* and *Antrodia carbonica*, the two most common basidiomycetes attack pine and Douglas-fir distribution poles. Although there was a reduction in the level of decay produced by *T. versicolor* over a twelve-week incubation period in a glass jar experiment, the *Trichoderma* treated poles were found susceptible to decay by *T. versicolor* in nature. These results and the earlier findings by Highley and Richard[32] clearly show that wood blocks pretreated with *Trichoderma* (Binab) were resistant to decay by BRF but offered little protection against WRF.

Bacteria as Biocontrol Agents

Bacteria, though major contributors to the decay of waterlogged wood, are much less important than fungi as agents of wood degradation[33] and as such do not represent a significant target for biological control systems. Over the past fifteen years, however, promising results have emerged by using bacteria to control sapwood-inhabiting blue-stain fungi[34-37]. Benko and Highley[38] evaluated the effectiveness of the bacterial cultures against blue stain and mold fungi as well as BRF and WRF. They used a mixed bacterial solution consisting of six bacteria from the genera *Pseudomonas* (*P. cepacia*), *Streptomyces* (*S. chrestomyceticus, S. rimosus* and *S. rimosus* forma *paromomycinus*), *Streptoverticillium* (*S. cinnamoneum* forma *azacoluta*), and *Xenorhabdus* (*X. luminescens*). The mixed bacterial culture was found strongly antagonistic against the wood-attacking fungi. Southern yellow pine (*Pinus* spp.) blocks treated with the solution of mixed bacterial culture suffered less than 1% weight loss after two months' exposure to the BRF (*Postia placenta*) or WRF (*T. versicolor*). Laboratory tests also indicated complete inhibition of blue-stain fungus, *Ceratocystis coerulescens* or mold, *Trichoderma harzianum* over the same period of time.

Actinomycetes as Biocontrol Agents

Over the past 55 years, actinomycetes have been the most widely exploited group of microorganisms in the production of secondary metabolites of commercial importance in medical and agricultural applications. Actinomycetes and particularly *Streptomyces* spp. are good sources of novel antibiotics, enzymes, enzyme inhibitors, immunomodifiers and vitamins. Their ubiquitous nature and prolific metabolic activity has led to 4,607 patents for actinomycetes-related products, including 3,477 antibiotics produced from *Streptomyces* alone[39,40]. Actinomycetes are Gram-positive, filamentous bacteria that are among the most abundant soil and rhizosphere microorganisms. Like filamentous fungi they grow with branching hyphae and can penetrate insoluble substrates, such as lignocellulose. Some of the examples of common genera of lignocellulose-degrading actinomycetes are *Streptomyces*, *Micromonospora*, *Microbispora*, *Thermomonospora*, *Norcardia* and *Arthrobacter* spp.[41,42]. Lignin degradation is a primary metabolic activity in the case of *Streptomyces* in contrast to *Phanerochaete chrysosporium*, where it is a secondary metabolic activity[43].

Streptomyces are important saprophytic soil microorganisms and well-known producers of antibiotics and extracellular enzymes[44]. They are primarily degraders of grass-type lignocelluloses.

Streptomyces spp. solubilize lignin but their mineralization of lignin to CO_2 is much less than that of other WRF[43,45,46]. This low wood lignin mineralization ability of *Streptomyces* spp. means that *Streptomyces* and other actinomycetes may be useful as biocontrol agents without much concern over their wood-decaying ability. Their biocontrol abilities clearly correlate with the production of antibiotics[47]. *Streptomyces violaceusniger* YCED9, for example, is a soil isolate which exhibits biocontrol activity against a variety of plant pathogenic fungi. The strain produces at least three antifungal antibiotics, including Nigericin, Geldanamycin and a complex of polyenes that includes Guanidylfungin A[15]. *Streptomyces* spp. are also known for their ability to cause lysis of fungal hyphae by producing chitinases and glucanases as already mentioned. The antifungal biocontrol agent, *S. lydicus* WYEC108 was capable of not only destroying germinating oospores of *Pythium ultimum* but also damaging the cell walls of the fungal hyphae[48]. WYEC108 also produced high levels of chitinases, induced to high levels as fungal cell walls are used as a carbon source in growth media. However, negligible levels of enzymes were detected when *S. lydicus* WYEC108 was grown in the absence of chitin. Chitinase production by *S. lydicus* WYEC108 was also induced by colloidal chitin, N-acetylglucosamine and chito-oligosaccharides. However, the synthesis was repressed by high (but not low) levels of glucose and carboxy methyl cellulose (CMC)[17].

Actinomycetes Fb352 was reported to possess antagonistic activity against fungi, *Aureobasidium pullulans* and *Hormonea dematodes*[49,50]. Many such reports are available in the literature that is related to the production of antibiotics antagonistic to several other fungi. These antibiotic substances induce malformations in fungi, such as stunting, distortion, swelling, hyphal protuberances or the highly branched appearance of fungal germ tubes, an indirect evidence to show antibiosis as a mechanism of antagonism. Using such criteria, it was detected that antibiotics of some soil actinomycetes caused similar effects on hyphae of *Helminthosporium sativum*, in culture and in soil. Several species from *Streptomyces violaceusniger* clade produced antifungal antibiotics, such as Niphithricin, Spirofungin, Azalomycin F complex, Guanidylfungins and Malonylniphimycin[51].

Soil and aquatic actinomycetes show considerable ability to survive starvation. Antibiotics and protein inhibitors are formed during the late growth cycle, when familiar regulatory processes, like transcriptional control, are ineffective. These secondary metabolites can prevent degradation of enzymes and structural proteins essential for survival as well as biosynthesis, which might form aberrant products during nutrient limitation. Interestingly, secondary metabolite production in S*treptomyces* spp. is subject to catabolic repression in the presence of high levels of carbon and nitrogen sources. Repression of secondary metabolite biosynthesis by ammonia or certain amino acids is common in actinomycetes. Nitrogen limiting conditions lead to the secretion of ligninases responsible for wood degradation by WRF, like *P. chrysosporium*. Low nitrogen conditions would also be conducive to the secretion of antifungal and antibacterial secondary metabolites by actinomycetes used as biocontrol agents[40].

Conclusion

Of all the potential biocontrol agents for use in controlling fungal wood decay, actinomycetes and particularly *Streptomyces* spp. are among the best sources of novel antifungal antibiotics, enzymes and enzyme inhibitors. Thus, they have great potential to be exploited as broad-spectrum biocontrol agent against wood biodeterioration caused by fungi. However, the future development of biological control systems for wood protection or treatment will ultimately depend on how they measure up against traditional chemical preservatives. New biological systems must perform well under field conditions; be competitive in terms of stability and product cost; be easy to apply, store and handle; and satisfy the same level of stringent testing and regulatory control which is required during the development of any new chemical wood preservative. Only when a biocontrol agent has fulfill all the above, the wood preservative industries can happily embrace the technology.

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Reference

1 Sedjo R A, Economic wood supply—Problems and opportunities: Choices for Canada's forest industry, *For Chron*, 2 (1990) 32.

2 Oberai C P, Forests for new millennium, *Employment News*, 24 (2000) 51.

3 Rauel K & Barnoud F, Degradation of wood by microorganisms, in *Biosynthesis and biodegradation of wood components*, edited by T Higuchi (Academic Press Inc. Florida) 1985, 441.

4 Kirk T K & Shimada M, Lignin biodegradation: The microorganisms involved, and the physiology and biochemistry of degradation by white-rot fungi, in *Biosynthesis and biodegradation of wood components*, edited by T Higuchi (Academic Press, Inc. Florida) 1985, 579.

5 Eriksson K E L, Blanchette R A & Ander P, Biodegradation of lignin in microbial and enzymatic degradation of wood and wood components (Springer-Verlag, New York) 1990, 225-232.

6 Niku-Paavola M L N, Karhunen E, Kantelinen A, Viikari L, Lundall T *et al*, The effects of culture conditions on the production of lignin-modifying enzymes by the white-rot fungus *Phlebia radiata*, *J Biotechnol*., 13 (1990) 211-221.

7 Bourbonnais R & Paice M G, Veratryl alcohol oxidases from the lignin-degrading basidiomycete *Pleurotus sajor-caju*, *Biochem J*, 255 (1988) 445-450.

8 Muheim A R, Waldner M S, Liosola A & Fiechter A, An extracellular aryl alcohol oxidase from the white-rot fungus *Bjerkendera adusta*, *Enzyme Microb Technol*, 12 (1990) 204.

9 Galliano H, Gas G & Boudet A, Biodegradation of *Havea brasililiensis* lignocellulose by *Rigidoporous lignosum*: Influence of culture conditions and involvement of oxidizing enzymes, *Plant Physiol Biochem*, 26 (1988) 619.

10 Perie F H & Gold M H, Manganese regulation of manganese peroxidase expression and lignin degradation by the white rot fungus *Dichomitus squalens*, *Appl Environ Microbiol*, 57 (1991) 2240.

11 Daniel G, Pettersson B, Nilsson T & Volc J, Use of immunogold cytochemistry to detect Mn(II)-dependent and lignin peroxidases in wood degraded by the white rot fungi *P. chrysosporium* and *Lentinula edoes*, *Can J Bot*, 68 (1990) 920.

12 Mcconnachie P R & Zahalsky A C, Immunological consequences of exposure to pentachlorophenol, *Arch Environ Health*, 46 (1991) 249.

13 Lippmann M, *Environmental toxicants*, 2nd edition (Wiley Interscience, New York) 2000, 725-739.

14 Trejo-Estrada S R, Sepulveda I R, Crawford D L, *In vitro* and *in vivo* antagonism of *Streptomyces violaceusniger* YCED9 against fungal pathogens of turf grass, *World J Microbiol Biotechnol*, 14 (1998) 865-872.

15 Trejo-Estrada S R, Paszczynski A & Crawford D L, Antibiotics and enzymes produced by the biocontrol agent *Streptomyces violaceusniger* YCED 9, *J Ind Microbiol Biotechnol*, 21 (1998) 81-90.

16 Kumar D & Gupta R K, Antagonistic *Streptomyces violaceusniger* to control wood-rotting fungi, in *Biodiversity and natural products: Chemistry and medical applications*, Conference, held on 26-31 Jan, 2004 (IUPAC International Conference, New Delhi, India) 2004, P-161.

17 Mahadevan B, Crawford D L, Properties of the chitinase of the antifungal biocontrol agent *Streptomyces lydicus* WYEC108, *Enzyme Microb Technol*, 20 (1997) 489-493.

18 Taylor R, Lelwellyn G C, Mayfield J E, Shortle W C & Dashek W V, Time-dependent appearance of extracellular polyphenol oxidase in relation to bimodal growth response of *C. versicolor* to catechol, in *Biodeterioration research I*, edited by G C Lelwellyn & C E O'Rear (Plenum Press, New York) 1987, 63-74.

19 Taylor R, Lelwellyn G C, O'Rear C E, Myfield J E, Smith K T *et al*, *In vitro* growth of *C. vesicolor*, a wood-decay fungus, responds differentially to catechol and tannic acid, in *Biodeterioration research II*, edited by G C Lelwellyn & C E O'Rear (Plenum Press, New York) 1989, 451.

20 Highley T L & Micales, J A, Effect of aromatic monomers on production of carbohydrate-degrading enzymes by white-rot and brown-rot fungi, *FEMS Microbiol Lett*, 66 (1990) 15-21.

21 Ramadevi, O K, Nagaveni H C, Raja M, & Sharma M N, Evaluation of the efficacy of Cashew nut shell liquid based products (CSNL) against termites and fungi, *Timber Dev Assoc*, 48 (3-4) (2002) 15-19.

22 Krishnan R V, Theagrajan K S, Ananthapadmanabha H S, Sharma M N, Prabhu V V *et al*, *Biocidal property of phenolic fraction of ethanol extractives of Hopea parviflora heartwood* (Int Res Group on Wood Protection, Sweden) 1993, Document No. IRG/WP/93-3003.

23 Papavizas G C, *Trichoderma and Gliocladium*: Biology, ecology, and potential biocontrol, *Annu Rev Phytopathol*, 23 (1985) 23-54.

24 Siefert K A, Brevil C, Rossignol L, Best M & Saddler J N, Screening for microorganisms with the potential for biocontrol of sapstain on seasoned timber, *Mater Org (Berl)*, 23 (1988) 1-12.

25 Ananthapadmanabha H S, Nagaveni H C & Srinivasan V V, *Control of growth of wood bio-deterioration by fungal metabolites* (Int Res Group on Wood Preserv, Sweden) 1992, Document No. IRG/WP/1527-92.

26 Highley T L & Ananthapadmanabha H S, Antagonistic properties of *Gliocladium virens* against wood attacking fungi(Int Res Group on Wood Preserv, Sweden) 1996, IRG/WP/1924-96.

27 Highley T L, Ananthapadmanabha H S & Howell C R, Control of wood decay by *Trichoderma* (*Gliocladium*) *virens*, *Mater Org (Berl)*, 31 (1997) 157-166.

28 Tronsmo A, Use of *Trichoderma* spp. in biological control of necrotrophic pathogens, in *Microbiology of the phyllosphere*, edited by N J Fokkema, & J V Heuvel (Cambridge University Press, UK) 1986, 348-362.

29 Morrell J J & Sexton C M, Evaluation of a biological agent for controlling basidiomycete attack of Douglas-fir and southern pine, *Wood Fibre Sci*, 22 (1990) 10-21.

30 Bruce A & Highley T L, Control of growth of wood decay basidiomycetes by *Trichoderma* spp. and other potentially antagonistic fungi, *For Prod J*, 41 (1991) 63-67.

31 Bruce A, King B & Highley T L, Decay resistance of wood removed from poles biologically treated with *Trichoderma*, *Holzforschung*, 45 (1991) 307-311.

32 Highley T L & Ricard J L, Antagonism of *Trichoderma* spp. and *Gliocladium virens* against wood decay fungi, *Mater Org (Berl)*, 23 (1988) 157-169.

33 Eaton R A & Hale M D C, *Wood decay, pests and protection* (Chapman & Hall, London) 1993.

34 Morrell J J & Sexton C M, Fungal staining of ponderosa pine sapwood: effects of wood preconditioning and bioprotectants, *Wood Fibre Sci*, 25 (1993) 322-325.

35 Benko R, Bacteria as possible organisms for biological control of blue stain, *International Research Group on Wood Preservation*, (1998) Document No.IRG/WP/1339.
36 Benko R, *Biological control of blue stain on wood with Pseudomonas cepacia 6253: laboratory and field test* (Int Res Group on Wood Preserv, Sweden) 1989, Document No. IRG/WP/1380.
37 Bernier R Jr, Desrochers M & Jurasek L, Antagonistic effects of *Bacillus subtilis* and wood staining fungi, *J Inst Wood Sci* , 10 (1986) 214-216.
38 Benko R & Highley T L, *Evaluation of bacteria for biological control of wood decay* (Int Res Group on Wood Preserv, Sweden) 1990, Document No.IRG/WP/1426.
39 Williams S T & Vickers J C, Detection of actinomycetes in the natural environment—Problems and perspectives, in *Biology of Actinomycetes*, edited by Y Okami, T Beppu & H Ogawara (Japan Scientific Societies Press, Tokyo) 1988, 265-270.
40 Demain A L, Control of secondary metabolism in actinomycetes, in *Proc Sixth Int Symp on Actinomycetes Biology*, edited by G Szabo, S Biro & M Goodfellow (Akademiae Kiado Press, Budapest) 1985, 215-225 [Demain, A L, *Biotechnol Adv*, 8 (1990) 291-301 & *Microb Biotechnol*, *TIBTECH*, 18 (2000) 26-31].
41 Finolow A B & Lockwood J L, Evaluation of several *Actinomycetes* and the fungus *Hypochytrium catenoides* as biocontrol agent for *Phytophthora* root rot of soyabean. *Plant Dis*, 69 (1985) 1033-1036.
42 Crawford D L, Lynch J M, Whipps J M & Ousley M A, Isolation and characterization of actinomycetes antagonist of a fungal root pathogen, *Appl Environ Microbiol*, 59 (1993) 3889-3905.
43 Wang Z, Crawford D L, Magnuson T S, Bleakley B H & Hertel G, Effects of bacterial lignin peroxidase on organic carbon mineralization in soil, using recombinant *Streptomyces* strains, *Can J Microbiol*, 37 (1991) 287-294.
44 Rothrock C S & Gottlieb D, Role of antibiosis in antagonism of *Streptomyces hygroscopicus* var. *geldanus* to *Rhizoctonia solani* in soil. *Can J Microbiol*, 30 (1984) 1440-1447.
45 Pasti M B, Pometo III A L, Nuti N P & Crawford D L, Lignin degrading ability of actinomycetes isolated from termite (Termitidae) gut, *Appl Environ Microbiol*, 56 (1990) 2213-2218.
46 Ruttimann C, Vicuna, R, Mozuch M D & Kirk T K, Limited bacterial mineralization of fungal degradation intermediates from synthetic lignin, *Appl Environ Microbiol*, 57 (1991) 3652-3655.
47 Hwang B K, Ahn S J & Moon S S, Production, purification and antibiotic activity of the antibiotic nucleoside, tubericidin produced by *Streptomyces violaceusniger*. *Can J Bot*, 72 (1994) 480-485.
48 Yuan W M & Crawford D L, Characterization of *Streptomyces lydicus* WYEC108 as a potential biocontrol agent against fungal root and seed rots, *Appl Env Microbiol*, 61 (1995) 3119-28.
49 Bezert G, Chappe P, Mourey A & Loubinoux B, Action de *Bacillus* et d'Actinomycetes sur les champignons de bleuissement du bois, *Comptes Rendus Acad Soc Lorraines Sci*, 35/3 (1996) 177-190.
50 Roussel C, Bezert G, Bucur V, Gerardin P, Loubinoux B *et al*, Evaluation of wood degradation during biological treatment with actinomycetes, *Holz als Roh-und Werkstoff*, 58 (2000) 127-128.
51 Getha K & Vikineswary S, Antagonistic effects of *Streptomyces violaceusniger* strain G10 on *Fusarium oxysporum* sp. *cubense* race 4: Indirect evidence for role of antibiosis in the antagonistic process, *J Ind Microbiol Biotechnol*, 28 (2002) 303-310.