Research Paper

Poly R decolorization and APPL production by *Streptomyces violaceoruber* and *Streptomyces spiroverticillatus*

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Abstract

Two mesophilic streptomycetes (*S. violaceoruber* and *S. spiroverticillatus*) were selected to study their Poly R-478 decolorization ability and lignocellulose solubilizing activity. Both strains were able to degrade Poly R-478 dye and ferulic acid during growth on a minimal salts medium. The Poly R-478 decolorizing activities of both strains were induced by adding different carbon sources to the culture media. *S. violaceoruber* could decolorize 63% of Poly R-478 after 24 h. Both strains could solubilize straw and produce acid-precipitable polymeric lignin (APPL) with different efficiency. From the major extracellular enzymes recovery of both strains on rice and wheat straw, we can predicate that the biodegradation process was partial indicating a possible utilization in biological delignification.

Key words: *Streptomyces*, APPL, Poly-R decolorization, ferulic acid degradation.

Introduction

There has been much attention focused on the exploitation of plant biomass as a renewable energy source (Van Wyk, 2001; Ragauskas *et al.*, 2006; Rubin, 2008). The bulk of plant biomass is lignocellulose, a complex of three polymers - lignin, cellulose, and hemicellulose (Rubin, 2008). It is generally accepted that lignin degradation is a rate-limiting step in lignocellulose degradation (Bisaria and Ghose, 1981; Himmel *et al.*, 2007). Therefore, the breakdown of lignin is critical for the conversion of this abundant form of biomass into high value chemicals or fuels as a source of renewable energy (Crawford 1981; Crawford *et al.*, 1984; Chen and Dixon, 2007; Abdel-Hamid *et al.*, 2013; Varanasi *et al.*, 2013).

Regarding environmental pollution, earlier reports confirmed that lignocellulose solubilizing organisms were also capable of decolorizing Poly R-478 and various triphenylmethane dyes (Ball *et al.*, 1989; Vasdev and Kuhad, 1994; Vasdev *et al.*, 1995). Biological decolorization method has been considered as effective, specific, less energy intensive and environmentally benign, since it results in partial or complete bioconversion of pollutants to stable nontoxic end products (Kuhad *et al.*, 2004; Sharma *et al.*, 2013).

Lignin depolymerization and catabolism have been studied in a number of bacterial species, including members of the *Streptomyces* (McCarthy, 1987; Zimmerman, 1990; Grund and Kutzner, 1998). There are many evidences that *Streptomyces* species may be useful in the utilization and bioconversion of lignin and lignin-derived aromatic compounds in biotechnological applications (Davis and Sello, 2010). Streptomycetes are of particular interest because of their apparent widespread ability to degrade the lignin of straw via formation of acid-precipitable polymeric lignin (APPL) intermediates (Ball *et al.*, 1989; Ball *et al.*, 1990; Mason *et al.*, 2001). APPL is a high molecular weight complex of lignin, carbohydrates and proteins and its relationship to lignin degradation need to be more understood.

Lignocarbohydrate solubilization by actinomycetes has been shown to be extracellular, and the involvement of a range of enzymes has been suggested (Ramachandra *et al.*, 1987; Deobald and Crawford, 1987; Donnelly and Crawford, 1988; Maciel *et al.*, 2010). These biocatalysts also represent potential application on environmental biocatalysis for the degradation of xenobiotics and recalcitrant pollutants (Gottschalk *et al.*, 2008; Sharma *et al.*, 2013).

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In this work, we aimed to evaluate the poly-R decolorization ability of *Streptomyces violaceoruber* and *Streptomyces spiroverticillatus*. In addition, we studied the APPL formation and the enzymology of the processes involved in the lignocarbohydrate solubilization to provide insights into the native lignin-solubilizing activity of these two actinomycetes.

Materials and Methods

Strains and growth conditions

Streptomyces violaceoruber and *Streptomyces spiroverticillatus* used in this investigation were isolated from a soil sample collected from Sinai-Egypt and identified according to International *Streptomyces* Project (Shirling and Gottlieb, 1968a, 1968b, 1969, 1972), Bergey's Manual of Determinative Bacteriology (Pridham and Tresner, 1974) and Bergey's Manual of Systematic Bacteriology (Locci, 1989). *S. violaceoruber* and *S. spiroverticillatus* stock spores were maintained at -20 °C in a 20% (w/v) glycerol aqueous solution in the laboratory of microbiology, Botany Department, Faculty of Science, Damietta University, Egypt. After cell growth at 30 °C for 5-7 days on starch-nitrate agar medium (Waksman, 1959), 1 mL of spores suspensions, containing about 8×10^6 spores of *S. violaceoruber* or *S. spiroverticillatus*; was used to inoculate shake flasks containing 50 mL minimal salts-yeast extract medium, pH 7.0; supplemented with 0.01%(w/v) ferulic acid or Poly R - 478. Other additive carbon sources (wheat straw, xylan, glucose) were added at 0.2% (w/v) concentration. For experiments on straw degradation, the medium was supplied with 1% (w/v) ball-milled rice or wheat straw. Minimal salts-yeast extract medium contained per 1 litre distilled water: yeast extract 2 g, $(NH_4)_2SO_4$ 0.1 g, NaCl 0.3 g, $MgSO_4.7H_2O$ 0.1 g, $CaCO_3$ 0.02 g and 1 mL trace element solution ($FeSO_4.7H_2O$ 1 g L^{-1}, $ZnSO_4.7H_2O$ 0.9 g L^{-1}, $MnSO_4.7H_2O$ 0.2 g L^{-1}). Cultures were incubated up to 14 days at 150 rpm and 30 °C.

Utilization of lignin related compound

Lignin related compounds, used as growth substrates, were ferulic acid and the polymeric dye Poly R - 478. Utilization of substrates was monitored spectrophotometrically after removing samples (0.1 mL) of culture medium at regular time intervals (up to 14 days). Decolorization of Poly R - 478 was determined according to Ball *et al.* (1989) by diluting samples 10 fold with distilled water. The wavelengths used for the absorbance ratios of Poly R - 478 were optical density at 518 nm and 346 nm (OD_{518}/OD_{346}). These wavelengths were chosen to produce the greatest change of the absorption ratio of Poly R - 478. Ferulic acid degradation was determined according to Ball *et al.* (1989) by diluting samples 100 fold with distilled water and recording optical density at 282 nm.

Determination of the lignin solubilizng activity of strains

Grown cultures on wheat and rice straw were centrifuged (5000 rpm for 20 min) and the supernatant was acidified to pH 1 to 2 with HCl. The acid-precipitated product (APPL) was removed by centrifugation (5000 rpm for 20 min), washed twice with distilled water, and finally dissolved in 0.05 M NaOH. APPL protein estimation by Bradford (1976) method (expressed as milligrams of protein per gram of straw) was used to monitor production.

Enzymes assay

Xylanase (endo-1,4-β-xylanase, EC 3.2.1.8) and cellulase (endo-1,4-β-glucanase, EC 3.2.1.4) activities were assayed by the estimation of reducing sugar released from oat spelt xylan and cellulose, respectively. The reaction mixture contained: 1 mL of 1.0% substrate dissolved in 0.1 M potassium phosphate buffer (pH 7.0) and 1 mL of diluted culture supernatant. The mixture was incubated at 50 °C for 10 min. The determination of reducing sugar released during the incubation mixture was detected by the dinitrosalicylic acid method of Miller (1959). 1 mL of dinitrosalicylic acid reagent was added to 1 mL of the clarified reaction mixture and standards. After mixing, the mixtures were boiled for 5 min. After cooling, the optical density of the coloured product at 550 nm was recorded. Calibration curves constructed using D-xylose or D-glucose standards in the range of 0- 5 μmole mL^{-1} were used. One unit of xylanase and cellulase activities were defined as the amount of enzyme that released 1 μmole of xylose and glucose respectively per millilitre per minute under assay conditions. Enzyme and substrate controls were included routinely.

Peroxidase (EC 1.11.1.x) assay was adapted from the assay developed by Ramachandra *et al.* (1987, 1988). Peroxidase was assayed using 2, 4-dichlorophenol (2,4-DCP) as substrate. The final reaction (4 mL) mixture contained potassium phosphate buffer (800 μL, 0.1 M, pH 7.0); 16 mM 4-aminoantipyrine (800 μL); 25 mM 2,4- dichlorophenol (800 μL); culture supernatant (800 μL) and 50 mM hydrogen peroxide (800 μL). The reaction was initiated by the addition of hydrogen peroxide which was added last. Samples were then incubated at 50 °C for 1.0 min. The increase in absorbance as a result of the oxidation of 4-aminoantipyrine was measured at 510 nm. One unit of enzyme activity was defined as the amount of enzyme required for an increase in absorbance of 1.0 unit mL^{-1}. Ferulic acid esterase FAE (feruloyl esterase, EC 3.1.1.73) assay, according to Garcia *et al.* (1998); contained 80 mg wheat bran incubated with culture supernatant (2 mL) and potassium phosphate buffer (2 mL, 0.1 M, pH 7.0). The assay was performed for 20 min at 50 °C, and the reaction was stopped by boiling samples for 3 min. The samples were then cooled and centrifuged (5 000 rpm, 10 min) and the

ferulic acid content of the supernatant determined by recording optical density at 282 nm. Calibration curve constructed using ferulic acid standard in the range of 0-5 μmole mL^{-1} were used. One unit of activity was defined as the amount of enzyme releasing 1 μmole ferulic acid per minute at pH 7.0 and 50 °C. Enzyme and substrate controls were included routinely.

Growth determination

The harvested mycelia of strains were used for determination of growth as intracellular protein content. Washed pellets were suspended in 20 mL of NaOH (1 M), and boiled for 20 min. Dilution of clarified solution was used to determine the intracellular protein concentration using Bradford method (1976). Bovine serum albumin was used as standard.

All incubations and assays were performed in triplicate. Results presented are the means of three replicates with standard errors.

Results

Poly-R decolorization ability

The results of the comparative studies on the ability of *S. violaceoruber* and *S. spiroverticillatus* to decolorize Poly-R, as a lignin related compound; indicated that both strains were able to decolorize Poly-R during growth on a minimal salts medium in which the dye represented the major carbon source. *S. spiroverticillatus* showed approximately linear reduction in Poly-R absorbance ratio over the first 48 h, about 35% decolorization; and no further decolorization occurred (Figure 1.). Unlike *S. spiroverticillatus*, *S. violaceoruber* revealed a repolymerization of Poly-R after decolorization (Figure 2.). However, *S. violaceoruber* could attain faster maximum decolorization (24 h compared with 48 h) and much higher (50% compared with 35%) relative to *S. spiroverticillatus.*

Improvement of poly-R decolorization ability

Generally, additive carbon sources, including glucose, xylan or wheat straw as a lignocellulose; were found to induce the decolorizing activities of both strains. Poly-R decolorization by *S. spiroverticillatus* grown on either glucose or xylan were found to follow a similar pattern of that without any additives (Figure 1). While the addition of these carbon sources to *S. violaceoruber* culture increased the maximum decolorization rate from 50% to about 58%. Additionally, it limited the repolymerization of Poly-R (Figure 2). Regarding wheat straw, it was found to be the most efficient additive carbon source to Poly-R decolorization. The activity of *S. spiroverticillatus* cultures additionally containing wheat straw was 1.5 to 3.5 times greater than those from other additive carbon sources examined at 24 h incubation period (Figure 1). The highest decolorization activity was obtained from *S. violaceoruber* culture
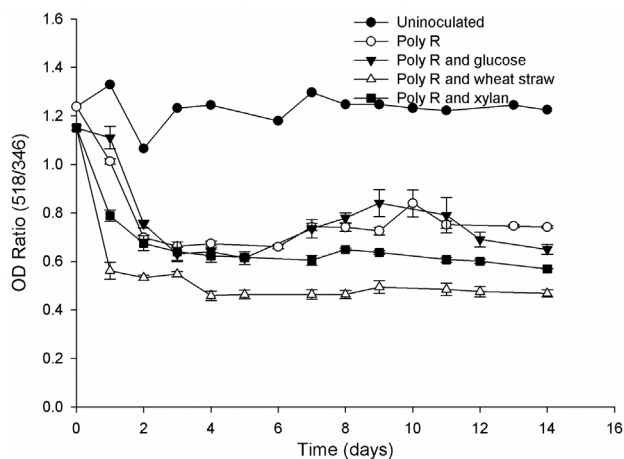

Figure 1 - Decolorization of Poly R, as measured by a decrease in the OD_{518}/OD_{346} ratio during the growth of *S. spiroverticillatus* on minimal salts-yeast extract media containing Poly R ($0.01\%_{w/v}$) or Poly R ($0.01\%_{w/v}$) in addition to xylan, glucose and wheat straw.

Figure 2 - Decolorization of Poly R, as measured by a decrease in the OD_{518}/OD_{346} ratio during the growth of S. *violaceoruber* on minimal salts-yeast extract media containing Poly R ($0.01\%_{w/v}$) or Poly R ($0.01\%_{w/v}$) in addition to xylan, glucose and wheat straw.
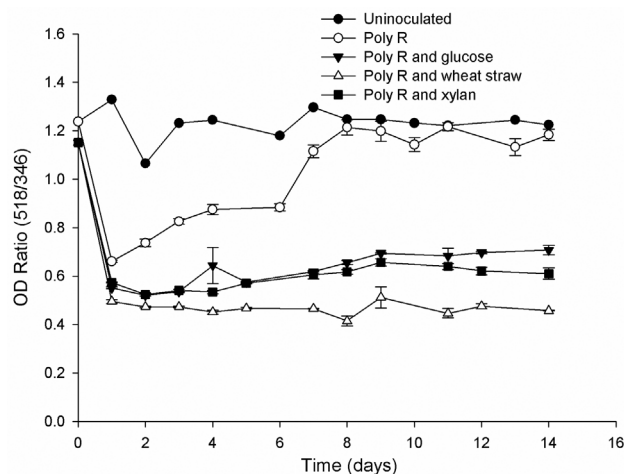
containing wheat straw as additive carbon source. In this case, decolorization rate reached the maximum rapidly (63% after 24 h) and then remained constant for the duration of the experiment (14 days) (Figure 2).

Wheat and rice straw solubilization

On the other hand, wheat and rice straw were used as native lignin sources. In general, wheat straw was more susceptible to solubilization by both *Streptomyces* strains as indicated by the yield of APPL. The present results with *S. violaceoruber* and *S. spiroverticillatus* showed a similar pH pattern during the incubation period with a trend to higher pH of 8.6. The peak activities for xylanase was approximately two to three fold for *S. violaceoruber* relative to *S. spiroverticillatus* (Table 1) and associated with the

growth phase. Also, the peroxidases production on wheat straw followed the same behaviour of xylanases. Whereas, the peaks of peroxidases activities for both strains cultured on rice straw were approximately the same. However, *S. violaceoruber* showed maximum activity about 7 days earlier than did *S. spiroverticillatus*. Interestingly, the present study showed that neither the amount of APPL production nor consumption was contributed to the production or stability of the major studied enzymes (Table 1).

Ferulic acid degradation

Although ligninolytic system of both strains was found to lack ferulic acid esterase, they could degrade ferulic acid and use it as a sole carbon source. In contrast to Poly-R degradation ability, *S. spiroverticillatus* was more able to degrade ferulic acid than *S. violaceoruber*. *S. spiroverticillatus* was able to degrade 56% of the ferulic acid in the culture after 24 h while *S. violaceoruber* could only degrade 37% after 10 days (Figure 3).

Discussion

The first experiment in this study is focused on decolorization of the polymeric dye, Poly-R. Decolorization of dyes may take place in two ways: either adsorption on the microbial biomass or biodegradation of the dyes by the cells (Zhou and Zimmermann, 1993). Biodegradation seems more natural in its operation while biosorption of dyes does not eradicate the problem. This is due to the difficult disposal of the microbial biomass containing adsorbed dyes (Chander and Arora, 2007). The dye decolorization by both *S. violaceoruber* and *S. spiroverticillatus* was attributed to biodegradation since the decrease in Poly-R absorbance was recorded as a ratio. In adsorption, examination of the absorption spectrum reveals that all peaks decrease approximately in proportion to each other but in the case of biodegradation, either the major visible light absorbance peak will completely disappear or a new peak will appear (Chen *et al.*, 2003; Saratale *et al.*, 2009).

Development of efficient dye degradation biotechnology requires application of a suitable selected strain under favourable conditions (Novotny *et al.*, 2004). The effectiveness of microbial decolorization depends on the adaptability and the activity of the selected microorganisms (Chen *et al.*, 2003). The most efficient class of microorganisms in breaking down dyes is the white-rot fungi (Couto, 2009; Maciel *et al.*, 2010). In comparison to fungal decolorization, decolorization by *S. violaceoruber* and *S. spiroverticillatus* is normally faster like other bacterial decolorization (Kalyani *et al.*, 2009; Maciel *et al.*, 2010). Interestingly, *S. violaceoruber* could decolorize Poly-R faster than the fungus *P. cinnabarinus*, 24 h compared with 192 h; with approximately the same efficiency and generally more efficient than *P. chrysosporium* (Diwaniyan *et al.*, 2010). In addition, percentage of decolorization of Poly-R by these two *Streptomyces* was more two folds

Table 1 - Production of APPL and major extracellular enzymes during rice and wheat straw degradation by *S. violaceoruber*, *S. spiroverticillatus* in agitated submerged cultures.

|	After 7 days							After 14 days						
	Intracellular protein (mg)	Final pH	Xylanase (U/mL)	Peroxidase (U/mL)	Cellulase (U/mL)	FAE (U/mL)	APPL production (mg protein per g straw)	Intracellular protein (mg)	Final pH	Xylanase (U/mL)	Peroxidase (U/mL)	Cellulase (U/mL)	FAE (U/mL)	APPL production (mg protein per g straw)
Rice straw														
S. violaceoruber	0.224 ± 0.061	8.09 ± 0.02	3.667 ± 0.27	0.067 ± 0.008	0.000	0.000	241.61 ± 10.65	-	8.61 ± 0.03	0.187 ± 0.044	0.068 ± 0.004	0.000	0.000	270.01 ± 4.5
S. spiroverticillatus	0.330 ± 0.044	8.01 ± 0.04	1.10 ± 0.277	0.045 ± 0.013	0.000	0.000	237.45 ± 23.27	-	8.59 ± 0.01	0.363 ± 0.038	0.061 ± 0.007	0.000	0.000	261.11 ± 1.59
Uninoculated control	0.000	7.00	0.000	0.000	0.000	0.000	177.88		7.00	0.000	0.000	0.000	0.000	224.98
Wheat straw														
S. violaceoruber	0.376 ± 0.036	8.07 ± 0.03	2.769 ± 0.742	0.068 ± 0.02	0.000	0.000	223.25 ± 15.59	-	8.56 ± 0.04	0.341 ± 0.172	0.000	0.000	0.000	225.9 ± 26.76
S. spiroverticillatus	-	8.04 ± 0.02	1.797 ± 0.147	0.031 ± 0.011	0.000	0.000	167.44 ± 15.17	-	8.58 ± 0.01	0.198 ± 0.019	0.002 ± 0.001	0.000	0.000	239.25 ± 3.74
Uninoculated control	0.000	7.00	0.000	0.000	0.000	0.000	109.76		7.00	0.000	0.000	0.000	0.000	142.92
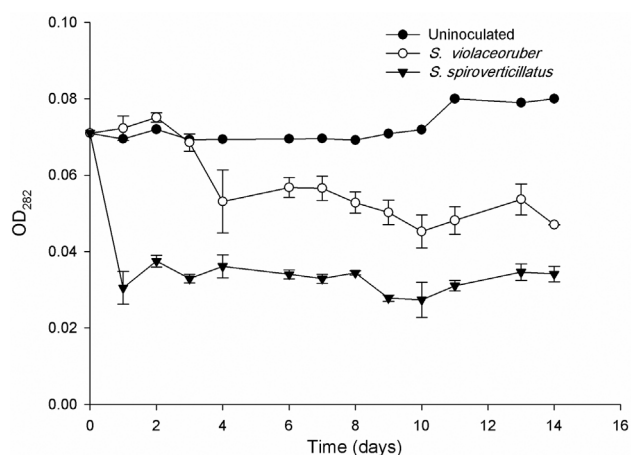
Figure 3 - Degradation of ferulic acid, as measured by a decrease in the OD$_{282}$ during the growth of S. violaceoruber, *S. spiroverticillatus* on minimal salts-yeast extract media containing ferulic acid (0.01%$_{w/v}$).

higher than that of the most widely studied *S. viridosporus* and *S. badius* (Ball and Colton, 1996; Ball *et al.*, 1989).

Furthermore, these strains were capable of utilizing Poly-R dye as sole source of energy for their growth which indicated a real elimination of the pollutant. However, Poly-R was repolymerized rapidly after strong and fast degradation by *S. violaceoruber.* This behaviour was improved by addition of carbohydrates. Kondo *et al.* (1990) showed that the presence of a glycosyl group facilitates the depolymerization of synthetic lignin and decrease repolymerization. Also, carbohydrates were reported to be essential for the mineralization of lignin models (Kirk *et al.*, 1976). It may play roles, in both levels, adaptability and activity of the organism. It could detoxify degradation products since the toxicity of the glycosides of these compounds is greatly reduced (Kondo and Imamura, 1989a) which improve the adaptability. On the other hand, the extracellular metabolites in presence of carbohydrates could contain other enzymes and certain compounds like organic acids, which would favour the decolorization process (Shah *et al.*, 2003; Wesenberg *et al.*, 2003) and prevent repolymerization of the radicals formed by the oxidative enzymes (Galliano *et al.*, 1991). In accordance with our results, Kondo and Imamura (Kondo and Imamura, 1989b) found that the rate of consumption of the lignin models was much faster in polysaccharide than in monosaccharide media.

Several studies indicated that only lignin-degrading microorganisms are able to decolorize polymeric dyes and that efficiency of decolorization is correlated with their ability to degrade several lignin model compounds (Chet *et al.*, 1985, Platt *et al.*, 1985). Ball *et al.* (1989) suggested that decolorization of polymeric dyes is a simple and rapid method to investigate the ligninolytic system in microorganisms. So it is not surprising that most commercially important dyes has a structural similarity to lignin (sub)structures, which are amenable to transformation by ligninolytic enzymes (Wesenberg *et al.*, 2003, Diwaniyan

et al., 2010). Therefore, the second experiment in this paper trended to study the biodegradation of native lignin by *S. violaceoruber* and *S. spiroverticillatus*. Since lignin is a complex polymer without a single repeating unit, and, moreover, contains bonds in a random three dimensional arrangement (Higuchi, 1985), it is very difficult to be degraded by common organisms. From the major extracellular enzymes recovery of *S. violaceoruber* and *S. spiroverticillatus*, we can predicate that it was partial biodegradation process. It is known that the basic xylanolytic reaction can only lead to complete hydrolysis of the hemicellulose component if enzymes attacking side-groups on the xylan chain and cross-links within lignocellulose (*e.g.* ferulic acid esterase) are also present. Ferulic acid esterase, in general; is rarely detected in streptomycetes. The possibility to explain that can be summarized in the lack of a complete set of xylanase enzymes, resulting in low and perhaps undetectable ferulic acid esterase activity (Garcia *et al.*, 1998). Interestingly, the complete absence of cellulases indicated a selective degradation of lignin with keeping the cellulosic biomass. Therefore, *S. violaceoruber* and *S. spiroverticillatus* could be used in biological delignification as a low energy and low cost pre-treatment. Because the components of rice straw are mainly cellulose and hemicellulose encrusted with lignin having in addition, only small amounts of protein (Parr *et al.*, 1992), rice straw was more resistant to *S. violaceoruber* and *S. spiroverticillatus* solubilizition compared with wheat straw.

Streptomycetes hydrolytic and oxidative enzymes act co-operatively in degradation of the lignocellulose complex during primary growth (Ball *et al.*, 1990). The mechanisms involved in this degradation process have not yet been fully elucidated. However, the main role is attributed to a solubilization activity rather than depolymerization (McCarthy, 1987). Generally, we may postulate that *Streptomyces* grows attached to straw which explain the undetectable growth in cases of low growth. The main product of straw and other lignocellulosic residues solubilization is an acid-precipitable polymeric lignin (Crawford *et al.*, 1983). In this study, lignocarbohydrate solubilization occurred during primary growth while the subsequent decrease in APPL yield suggests further degradation or modification of solubilized material. Different cases of APPL degradation by ligninolytic streptomycetes has been reported by Pometto and Crawford (1986) who considered that an additional evidence for diverse lignocarbohydrate solubilizing patterns among streptomycetes (Borgmeyer and Crawford, 1985). On the other hand, Haemmerli *et al.* (1986) found that repolymerization occurred when the rate of peroxidase catalysis was high. Also Nanayakkara *et al.* (2014) reported the repolymerization of depolymerized oligomeric lignin and explained it by the esterification of hydroxyl groups in the oligomeric products. This fact may be postulated in the case of culturing

both *S. violaceoruber* and *S. spiroverticillatus* on rice straw but needs to be confirmed further.

In accordance with the ability to degrade native lignin and Poly-R dye, *S. spiroverticillatus* have strong and fast ability to metabolize ferulic acid which is naturally linked with hemicellulose by ester bond (Mueller-Harvie *et al.*, 1986; Smith and Hartleyr, 1983). However, they couldn't release it from straw due to the lack of ferulic acid esterase.

The reported results here provide evidence that *S. violaceoruber* and *S. spiroverticillatus* may be useful in the biological delignification of lignin in biotechnological applications as a low energy and low cost pre-treatment. Regarding environmental pollution, this study suggests *S. violaceoruber,* as a suitable strain to develop an efficient Poly-R degradation biotechnology.

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