Abstract: In recent years, the importance of biomass utilization has increased, but it has not been effectively exploited. In particular, it is difficult to use hemicellulose, the second most abundant biopolymer of biomass. Therefore, in order to promote the utilization of hemicellulose, we screened for microorganisms capable of producing polysaccharides from D-xylose. The following four strains were selected from samples collected from various regions of Okinawa Prefecture: Kosakonia sp. (SO_001), Papiliotrema terrestris (SO_005), Pseudarthrobacter sp. (SO_006), and Williamsia sp. (SO_009). Observation with a scanning electron microscope (SEM) confirmed that each bacterium produced polysaccharides with different shapes. In addition, the molecular weight and sugar composition of the polysaccharides produced by each bacterium were distinct. The selected microorganisms include closely related species known to promote plant growth and known to suppress postharvest pathogens. Since these microorganisms may be used not only in known fields but also in new fields, the results of this research are expected to greatly expand the uses of hemicellulose.

Key words: extracellular polysaccharides, pentose bioconversion, Kosakonia, Papiliotrema, Pseudarthrobacter, Williamsia

INTRODUCTION

The plant cell wall is the most abundant resource on earth. Thus, many attempts have been made to utilize plant cell walls to produce useful substances such as fine chemicals, food materials, fibers, feeds, fertilizers, and fuels in order to become independent from the fossil fuel oil and to curb greenhouse gas emissions. The plant cell wall is the most abundant resource on earth. Wall materials, fibers, feeds, fertilizers, and fuels in order to produce useful substances such as fine chemicals, the plant cell wall is the most abundant resource on earth. Hemicellulose has limited utility, and it is used in very small amounts relative to its abundance. One of the factors that hinders the synthesis of bioproducts from hemicellulose is that hemicellulose is heterogenous and it contains pentose as a main component. Pentose is difficult to use for nanofiber and ethanol synthesis because it has one less carbon than D-glucose (D-Glc). Therefore, we aimed to convert hemicellulose into a biologically useful substance. There have been several past attempts at hemicellulose bioconversion into ethanol, xylitol, 2,3-butanediol, lactic acid oil, various chemicals, or anionic monomers. In this study, we targeted the polysaccharides as hemicellulose bioconversion. After screening for microorganisms capable of producing polysaccharides from D-xylose (D-Xyl), we found several microorganisms that produced polysaccharides using only D-Xyl as a carbon source. Subsequently, we analyzed the properties of these microorganisms and the polysaccharides that they generated.

MATERIALS AND METHODS

Screening. The microorganism sources were collected from various regions of Okinawa Prefecture, Japan. After suspending 1 g of the collected water or soil sample in sterilized tap water, it was diluted appropriately and inoculated onto 1.5 % (w/v) agar plates containing 2 % (w/v) D-Xyl, 0.7 % (w/v)
K$_2$HPO$_4$, 0.3 % (w/v) KH$_2$PO$_4$, 0.05 % (w/v) sodium citrate, 0.1 % (w/v) (NH$_4$)$_2$SO$_4$, and 0.02 % (w/v) MgSO$_4$·7H$_2$O. Colonies that produced viscous substances (visually confirmed) were chosen, and the method was repeated until we obtained pure colonies.

**Analysis.** The BioJet Company, Ltd. (Uruma, Okinawa, Japan) analyzed the genomic DNA of the selected bacteria. The characteristics of the selected strains were tested using API20NE, APIZYME, and API50CH kits according to the manufacturer’s instructions (Biomerieux SA, Lyon, France). For lipid analysis, whole lipids from selected strains were extracted and methylated according to protocols from a previous report. The lipids were then analyzed with a GC-2010 gas chromatography system (Shimadzu Co., Kyoto, Japan) and a DB-WAX column (Agilent Technologies Inc., Santa Clara, CA, USA) using the Food Industry FAME 37 mix (30 mg/mL total in methylene chloride) (GL Sciences Inc., Shinjuku, Tokyo, Japan) as a standard according to the application note from Agilent Technologies (5989-3760JAP).

Three-ml of medium containing 2 % (w/v) D-Xyl, 0.7 % (w/v) K$_2$HPO$_4$, 0.3 % (w/v) KH$_2$PO$_4$, 0.05 % (w/v) sodium citrate, 0.1 % (w/v) (NH$_4$)$_2$SO$_4$, and 0.02 % (w/v) MgSO$_4$·7H$_2$O was dispensed into falcon tubes. Each strain was inoculated to the medium and cultured at 30 $^\circ$C for 72 h. The resulting culture was diluted with sterilized water to OD$_{600}$ = 1.0, and 1 mL of each bacterial suspension was inoculated into a 500 mL baffled Erlenmeyer flask containing 100 mL of medium and cultured at 30 $^\circ$C, 170 rpm for 72 h. The resulting culture was diluted with sterilized water to OD$_{600}$ = 1.0, and 1 mL of each bacterial suspension was inoculated into a 500 mL baffled Erlenmeyer flask containing 100 mL of medium and cultured at 30 $^\circ$C, 170 rpm for 72 h. After the culture supernatant was obtained by centrifugation (15,000 × G, 45 min, 4 $^\circ$C), the supernatant was heated at 100 $^\circ$C for 1 h, and centrifuged again (15,000 × G, 45 min, 4 $^\circ$C). The supernatant was dialyzed against distilled water for 3 days, centrifuged (15,000 × G, 45 min, 4 $^\circ$C), and freeze-dried, then subjected to the following analysis.

The sugar compositions of the produced polysaccharides were hydrolyzed with 2 M trifluoroacetic acid at 120 $^\circ$C for 1 h and then the hydrolysates were analyzed by high-performance anion-exchange chromatography with a pulsed amperometric detection (HPAEC-PAD) system (Thermo Fisher Scientific Inc., Waltham, MA, USA). The neutral sugars were analyzed using a Carbo-PacPA-20 column (Thermo Fisher Scientific) with a flow rate of 0.5 mL/min and elution with 2 mM NaOH (0-15 min), followed by a stepwise gradient of 200 mM NaOH (15-25 min). The acidic sugars were analyzed using a Carbo-Pac PA-1 (Thermo Fisher Scientific) column (3 × 150 mm) as described previously.

The weight average molecular weight (Mw) of the produced polysaccharides were determined by size exclusion chromatography using a LC-2000Plus liquid chromatograph with the refractive index detector (JASCO International Co., Ltd., Hachioji, Tokyo, Japan) and a Sephacryl S-500 HR 10/30 column (Cytiva, Tokyo, Japan), eluted with distilled water at a flow rate of 0.4 mL/min. The column was calibrated with pullulan narrow Mw standards (Mw 50,000, 200,000, and 800,000) (Sigma-Aldrich, St. Louis, MO, USA).

The Fourier transform infrared spectroscopy (FT-IR) spectra of the polysaccharides were measured using an FT-IR-8000 spectrophotometer (JASCO) in transmittance mode from 4,000 to 400 cm$^{-1}$ in a KBr disc. The KBr disc was prepared by dispersing the solid sample in KBr salt.

Scanning Electron Microscope (SEM) images of the strains were obtained according to the following procedure. Each sample was immersed in 2.5 % (v/v) glutaraldehyde in 0.1 M sodium phosphate buffer, pH 7.4 followed by an overnight incubation at 4 $^\circ$C. Thereafter, the suspensions were applied dropwise on a polycarbonate membrane filter (pore size: 0.6 µm). The samples on the filter were rinsed three times with 0.1 M sodium phosphate buffer, pH 7.4. Next, the samples were post-fixed for 1 h at 25 $^\circ$C in osmium tetroxide (1.0 %) and 0.1 M sodium phosphate buffer, pH 7.4. The samples were then rinsed three times in 0.1 M sodium phosphate buffer, pH 7.4. Next, the samples were dehydrated in a graded series of ethanol for 15 min at each step. Subsequently, the samples were dried in a critical point dryer (SYSGLC-8, Sanyu-Gijutsu Co., Ltd., Akiruno, Japan) at 40 $^\circ$C with a purging flow rate of 1.0 L/min. The dried samples were coated with osmium (1.5 nm) using an osmium plasma coater (HPG-20, Vacuum Devise Co., Mito, Japan). The coated samples were observed under a SEM (JSM-7900F, JEOL Ltd., Akishima, Japan) at an accelerating voltage of 1 kV. The images were obtained using a secondary electron detector.

**RESULTS AND DISCUSSION**

**Characteristics of obtained strains.** We obtained 15 strains producing viscous substances on media containing D-Xyl as the sole carbon source. The 16S rDNA sequences of each strain were analyzed and similar bacteria were omitted. Finally, we selected the following four strains: SO_001, SO_005, SO_006, and SO_009 (As a result of SEM, the size of SO_005 was considerably larger than others, suggesting the possibility that it is not a bacterium.). Each genomic sequence was analyzed by extracting an arbitrary 3 kb sequence from the longest contig of the de novo assembly of each microorganism and BLAST analysis was performed. This analysis generated a highly homologous genomic sequence that was downloaded and mapped. SO_001 had a maximum mapping rate of 94.0 % for Kosakonia radiicincentis GXGL, SO_005 was not applicable, SO_006 had a maximum mapping rate of 54.2 % for Pseudarthrobacter chlorophenolicus A6, and SO_009 had a maximum mapping rate of 15.5 % for Gordonia bronchialis strain FDA ARGOS_676. SO_006 and SO_009 were judged to be novel and dissimilar to known bacteria. Since SO_005 was not applicable, a BLAST search was performed with the maximum depth contig of the de novo assembly. This analysis generated a highly homologous genomic sequence that was downloaded and mapped. This genomic sequence shared 99.8 % identity with Papiliotrema terrestris 28S rDNA. The 16S rDNA sequence of SO_001 was 98.9 % identical with Kosakonia oryzae Ola51, the 16S rDNA sequence of SO_006 showed 97.7 % identity with Arthrobacter enciensis NIO-1008, and the 16S rDNA sequence of SO_009 was 98.8 % identical with Williamsia marianensis DSM44944. From these results, SO_001 was identified as Kosakonia sp., SO_005 was identified as P. terrestris, SO_006 was identified as Pseudarthrobacter sp., and
SO_009 was identified as *Williamsia* sp. Since the 16S rDNA of SO_006 was less than 98.7% identical to any known species, it is likely a new species. Genomic analysis using MiFuP Safety (National Institute of Technology and Evaluation, Kazusa, Chiba, Japan) revealed that these microorganisms did not contain any gene regions with harmful properties. In a previous report, several bacteria have been identified which potentially catalyze the bioconversion of hemicellulose into polyanionic heteropolysaccharide. These candidate bioconverters include *Cryptococcus laurentii*, *Klebsiella pneumoniae*, *Arthrobacter viscosus*, and *Pseudomonas* ATCC 31260. Interestingly, the identified strains in this study were different from those described in the previous report.

Figure 1 shows the SEM images of the four selected strains. SO_001, SO_006, and SO_009 are bacilli, but their morphologies are different. In SO_001, a substance that appears to be a long filamentous polysaccharide was observed. In contrast, the SO_009 images lack the thread-like substance, but a sticky substance was observed that clung to the bacteria. SO_006 was different from SO_001 and SO_009 and had a shape that resembled a silk moth cocoon. In addition, a thread-like substance thinner than that observed with SO_001 was present in the SO_006 image. SO_005 had a spherical shape and was covered with a thin thread-like substance.

The strains grew well at 30–35 °C and pH 5.5–7.5 (SO_001), 30–35 °C and pH 6.0–9.0 (SO_005), 30 °C and pH 6.0–9.0 (SO_006), as well as 30 °C and pH 5.0–6.0 (SO_009).

The characteristics of the strains are summarized in Table 1. The sugar metabolism results differ between the API50CH and API20NE kits, probably because the protocols are different. Since the API20NE kit is designed for determining the bacterial species and the API50CH kit is designed for examining sugar metabolism, the sugar metabolism results from the API50CH kit are considered to be highly reliable.

The API50CH kit results showed that a considerable number of items were negative for strains other than SO_001. It was considered that the growth rate of the strains was slightly slower compared to SO_001. This is also supported by the fact that strains other than SO_001 have a negative D-Xyl assimilation property. Since all of the sugar items of SO_009 (including glucose) was negative, it was suggested that the metabolic rates of D-Xyl and D-Glc of this strain does not much different.

The lipid analysis results are shown in Supplemental Table S1 and Fig. S1; see J. Appl. Glycosci. Web site. The lipid analysis appeared to capture the characteristic cellular fatty acid content of closely related strains of each species. However, it was not entirely clear due to the lack of standards. Related species of SO_005 (*Papilio-trema laurentii*) was known to produce lipids from D-Xyl, and studies on productivity and lipid composition were investigated.

**Characteristics of polysaccharides.**

Next, the viscous substances produced by the selected strains were analyzed. The results of FT-IR analysis are shown in Fig. 2. Basically, all the samples have similar shapes. In each case, peaks characteristic of saccharides (3,500–3,200 cm⁻¹ corresponding to hydroxyl groups,
1,600–1,725 cm$^{-1}$ corresponding to carboxyl groups, and 1,150–1,000 cm$^{-1}$ corresponding to CO) were detected.

When the Mw was measured by gel filtration chromatography using pullulan as a standard, SO_001 was divided into at least three peaks, with Mws of $4.5 	imes 10^6$, $3.6 	imes 10^6$, and $1.3 	imes 10^6$, respectively. The Mw of SO_005 was $5.9 	imes 10^6$, SO_006 was divided into three peaks with Mws of $4.4 	imes 10^6$, $2.6 	imes 10^6$, and $1.7 	imes 10^6$, and the Mw of SO_009 was $4.4 	imes 10^6$, respectively. SO_005 was comprised of only one peak, but the Mw of the polysaccharide heteropolymer ($2.37 	imes 10^6$) produced by Papilioatrema flavescens was divided into four peaks by anion exchange chromatography. Therefore, the polysaccharide of SO_005 may be a mixture of several polysaccharides. However, since the Mw of SO_005 is very different from the reported Mw of *P. flavescens*, a detailed examination is required in future to discriminate between the two.

Table 2 summarizes the results from the sugar composition analysis of the polysaccharides produced by the obtained strains. The polysaccharide of SO_001 contained 24 % D-Glc, 37 % D-galactose (D-Gal), 31 % L-fucose (L-Fuc), and 8 % D-glucuronic acid (D-GlcA). The L-Fuc-rich polysaccharide of *Kosakonia sp.* CCTCC M2018092 had a molecular mass of $3.65 	imes 10^5$ Da, which is approximately 10 times smaller than that of SO_001. The partial acid-hydrolyzed L-Fuc-rich polysaccharide is composed of L-Fuc, D-Glc, D-Gal, D-GlcA and pyruvic acid with a molar ratio of 2.03: 1.00: 1.18: 0.64: 0.67, and suggested that the
The sugar composition of the SO_006 polysaccharide is 53 % D-Glc, 12 % D-Gal, 11 % L-Fuc, 20 % D-Man, and 3 % D-GlcA. Arthrobotacter viscosus has been reported to produce heteropolysaccharides using D-Xyl and xylooligosaccharides as carbon sources. The polysaccharides synthesized by the strain ranges in size from 6 × 10^5 Da to 1.5 × 10^6 Da depending on the carbon source. In contrast, the polysaccharide of SO_006 appears to be the same size as that of A. viscosus or several times larger. The polysaccharides from A. viscosus are acetylated and composed of < 30 % D-Glc, approximately 30 % D-Gal, and < 20 % D-mannuronic acid (D-ManA) with a repeating unit of O-β-D-ManpA-(1→4)-β-D-GlcA-(1→4)-D-Galp-(1→). Since the SO_006 polysaccharide does not contain D-ManA and contains 11 % L-Fuc, 20 % D-Man, and 3 % D-GlcA, it is expected that it has a different structure from that of A. viscosus. The sugar composition of the SO_009 polysaccharide is 42 % D-Glc, 31 % D-Gal, 13 % D-Man, and 14 % D-GlcA. However, the polysaccharides from the Williamsia genus remain uncharacterized. Therefore, the structure of the SO_009 polysaccharide remains unknown.

**Conclusions.**

D-Xyl, which is a constituent of xylan, is the second most abundant sugar on earth. D-Xyl is difficult to use due to its low conversion efficiency to ethanol, and it is rarely used except for food applications such as a sweetening agent or a brewing agent. We have focused our research on the use of enzymes for hemicellulose (with its heterogeneous structure) degradation. We anticipate that the utility of hemicellulose will be expanded because the hemicellulose-degrading enzymes can precisely identify the structures of the hemicellulose substrates. Recently, we have revealed the substrate specificity of β-xylanases for branches in xylan, and have shown the possibility to produce various branched oligosaccharides in combination with xylanase. In this method, the monosaccharide D-Xyl is generated as a by-product of the branched oligosaccharide. The four strains that we discovered in this study, which can produce polysaccharides using D-Xyl as the sole carbon source, are promising as one of the ways to utilize generated D-Xyl. Thickening polysaccharides have various applications including food ingredients, cosmetics, pharmaceuticals, bioplastics, and nanocomposites, etc. which are dependent on their physical characteristics. Most of the polysaccharides currently used in industry are derived from plants and seaweeds, while very little are derived from microorganisms. Although plant cultivation is affected by harvest time and environmental conditions, microorganisms can produce polysaccharides throughout the year and are not affected by climate. Therefore, microorganism-mediated synthesis of polysaccharides can be scaled up and can be used in fields such as “materials” and “fuel” (for example, shale gas fractur-
ing) which comprises a large market. In fact, it has been reported that the properties of hydrogels can be improved by adding glucuronoxylomannan (produced by *Papiliotrema*) to alginic acid.\(^{27}\) In addition, *Kosakonia* sp. is a plant growth promoting bacteria, and it is being used to generate polysaccharides which may function as plant growth promoters.\(^{28}\) \(^{29}\) *P terrestris* is a biocontrol agent that protects against postharvest pathogens. Therefore, we anticipate that the polysaccharides produced by the microorganisms found in this study may be used in an environmentally friendly manner to promote the growth of plants which can fix carbon dioxide. We also hope that these microorganisms protect these plants from harmful microorganisms.

Thus, our findings potentially expand the utility of hemicellulose. In future studies, we would like to explore how to use the polysaccharides produced by the microorganisms discovered in this study to further enhance the use of hemicellulose.

CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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