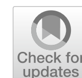
Current Microbiology (2020) 77:3460–3472
https://doi.org/10.1007/s00284-020-02160-7



Isolation and Selection of *Streptomyces* Species from Semi-arid Agricultural Soils and Their Potential as Producers of Xylanases and Cellulases

Y. E. Castañeda-Cisneros[1] · Y. Mercado-Flores[1] · M. A. Anducho-Reyes[1] · J. Álvarez-Cervantes[1] · B. Ponce-Lira[2] · Z. Evangelista-Martínez[3] · A. Téllez-Jurado[1]

Received: 24 February 2020 / Accepted: 6 August 2020 / Published online: 14 August 2020
© Springer Science+Business Media, LLC, part of Springer Nature 2020

Abstract

The Mezquital Valley (MV), Mexico, is a semi-arid region whose main economic activity is agriculture, this zone is characterized by the use of wastewater for crop irrigation. This condition has increased the amount nutrients in soils, organic carbon content and native microorganisms. The *Streptomyces* species are a group of saprophytic bacteria that represent between 20 and 60% of the total microbial population in soils, capable of producing metabolites of commercial importance. In this work, *Streptomyces* species were isolated from agricultural soils of the MV and was evaluated the production of endoglucanases (CMCase) and xylanases (Xyl) in Solid-State Cultivation (SSC). From soil samples, 73 possible strains of *Streptomyces* species were isolated for their ability to produce CMCase and Xyl in SSC. The study also included its characterization by morphological characteristics. Of the isolated microorganisms, 38 strains were selected as strong enzyme producers according to the measurement of the halo generated in plate and by growth on barley straw as only carbon source. Two different sizes of barley straw particle were tested, finding that the greatest enzymatic activity was observed in particle size 12. Three strains of *Streptomyces* species were chosen which presented the best catalytic capacities, a maximum of 100.69 AU Xyl/gram dry matter (gdm), 82 AU Xyl/gdm and 26.02 AU CMCase/gdm for strains 30, 28 and 12, respectively. The strains were identified by ribosomal gen16s sequence and identified as *S. flavogriseus*, *S. virginiae* and *S. griseoaurantiacus*. It is the first report of endogluconase and xylanolytic activity by *S. virginiae* isolated from a semi-arid soil.

Introduction

The word "Actinomycetes" is derived from the Greek "atkis" (ray) and "mykes" (fungus), that is, it has characteristics of bacteria and fungi [1]. These microorganisms produce aerobic spores, they are gram-positive bacteria; with high guanine-cytosine content (57–75%) in its genome, and belong to the order Actinomycetales characterized by the growth of aerial mycelium and substrate [2, 3]. Actinomycetes are present in various ecological habitats, are common organisms in soils [4, 5], especially in dry soils, slightly acidic soils, rich in organic matter and represent a high proportion of total microbial biomass [6]. These microorganisms are characterized by generating a great diversity of bioactive metabolites that are highly appreciated in the biotechnology industry [7, 8]. Of the approximately 18,000 known bacterial compounds, more than 10,000 were isolated from bacteria of the genus *Actinomyces* and *Streptomyces* [9].

Soil actinomycetes have been a myriad source of secondary metabolites, including antibiotics, anti-cancer,

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00284-020-02160-7) contains supplementary material, which is available to authorized users.

✉ A. Téllez-Jurado
alito@upp.edu.mx

[1] AgroBiotechnology Laboratory, Polytechnic University of Pachuca, Carr. Pachuca-Cd. Sahagún, km 20, Ex-Hacienda de Santa Bárbara, C.P. 43830 Zempoala, Hidalgo, Mexico

[2] Department of Agrobiotechnology Engineering, Polytechnic University of Francisco I. Madero, Carretera Tepatepec-San Juan Tepa, C.P.42660 Francisco I. Madero, Hidalgo, Mexico

[3] Centro de Investigación y Asistencia en Tecnología y Diseño del Estado de Jalisco. AC, Parque Científico Tecnológico de Yucatán, Sierra Papacal-Chuburná Puerto, C.P.97302 Mérida, Yucatán, Mexico

immunosuppressants, pigments, herbicides and enzymes [10, 11], however the frequency of discovery of novel compounds is decreasing in these years and the findings seem to imply that the easily accessible microorganisms in the soil have been depleted and that there is a need to opt for unexplored or under-explored sources [12, 13]. It is believed that ecological and environmental conditions influence the metabolic capacity of bacteria for the production of secondary metabolites [14]. In this context, the exploration of new habitats is one of the most promising ways to isolate new actinomycete species that will probably lead to the discovery of potentially beneficial new metabolites. It has been described that extreme habitats induce microorganisms to produce more stable enzymes, representing an economic advantage for biotechnological processes [15]. Furthermore, the interaction between different species or genera of microorganisms results in large amounts of metabolites being secreted that fulfill different functions, one of which is to participate in their adaptation [16]. For example, it has been described that microorganisms that grow in alkaline soils tend to fix phosphorus more efficiently [17]. Therefore, it is of interest to study microorganisms that are capable of growing in extreme habitats, which would increase the probability of finding no-common metabolites such as enzymes. More recently, there has been a growing interest in exploring arid and semi-arid environments, where bacteria are exposed to drying conditions, high salinity and UV radiation [18].

The actinomycetes of arid and semi-arid regions have been studied for several authors, for example: Aouar et al. [19], identified 72 actinomycetes from semi-arid soils associated with the rhizosphere of cereals, trees and vegetables in Algeria in order to evaluate its capacity for biological control in phytopathogenic fungi through the secretion of antifungal compounds and chitinolytic enzymes. Korayem et al. [20], isolated 50 actinomycetes of the genus *Streptomyces* from arid soils in Egypt and determined lipolytic activity and biosurfactant production. Yeager et al. [21], examined the potential of 112 strains of actinomycetes isolated from a semi-arid prairie belonging to Colorado, Utah, they detected enzymatic activities of endocellulase, xylanase, pectinase and chitinase using hydrated herbal extracts as substrate.

The MV region represents a particular ecosystem located southeast of the Hidalgo state, Mexico. This area is the largest block of land in the world where untreated sewage has been used for agricultural irrigation for more than a century [22]. The climate is semi-arid with an average annual temperature of 15–17 °C and an average annual rainfall of 400–600 mm [23]. In addition, it is considered one of the most polluted regions in Mexico due to the presence of chemical, cement, refinery and thermoelectric industries [24]. The reports on the analysis of microbial communities in this region are limited with the exception of two works previously carried out by pyrosequencing, the first is that of Broszat et al. [25] determined the influence of the use of residual water on the bacterial communities of agricultural soils of the VM, they found that over the years certain bacterial communities were benefited (Actinobacteria 27.4%, Proteobacteria 14.6% and Acidobacteria 14%), probably due to the supply of organic matter through wastewater. And the second, reported by Lüneberg et al. [26], where the impact on the composition of bacterial communities of irrigated MV soils with different qualities of water (fresh water, untreated wastewater stored in dams and water untreated residual) was evaluated. These authors suggest that the diversity of soils is due to the specific adaptations of each lineage. The bacterial taxa associated with the soil irrigated by wastewater are adapted to higher concentrations of sodium ions, presence of surfactants and heavy metals.

Studies of the microbial communities present in MV soils have been carried out, but there are no studies focused on the isolation of *Streptomyces* species or of the enzymes production. In this study, isolated *Streptomyces* species from two semi-arid agricultural soils of the MV were characterized and evaluated to determine the production of endogluconase (CMCase) and xylanase (Xyl) enzymes in solid-state cultivation. The strains that presented the highest enzymatic activities were molecularly identified.

Materials and Methods

Study Area

Composite samples of rhizosphere of agricultural soils were collected in the semi-arid region of the MV, Hidalgo, Mexico. The first site was a barley crop with wheat rotation in Cinta Larga, Mixquiahuala (20° 13′ 46.9″ N, 99° 05′ 21.23″ W,) and the second a corn crop with oat rotation in Francisco I. Madero, Hidalgo, México (20° 13′ 20.45″ N, 99° 05′ 28.82″ W), the specifications of Mexican Standard [27] were used for sampling, soil samples were taken at a depth of 10–20 cm. The samples were transported to the laboratory in sealed plastic bags at 4 °C, for later analysis.

Streptomyces Species Isolation

The method used for the isolation of *Streptomyces* species was that of serial dilutions [28]. One gram of dry soil from each sample was vigorously stirred in 9 mL of sterile distilled water and preheated at 50 °C for 30 min [29]. This solution (10^1) was diluted five times (10^5) using sterile distilled water. An aliquot of 50 µL was taken which were distributed on plates of two culture media: Agar yeast extract-malt extract ISP2 (Yeast extract 4 g/L (Dibico), extract 10 g/L malt (Dibico), 4 g/L dextrose (Sigma) and 20 g/L bacteriological agar at pH 7.3) and ISP3 oat agar

(20 g/L oat and 18 g/L bacteriological agar (Dibico) at pH 7.2) supplemented with nystatin (50 μg/mL) and nalidixic acid (25 μg/mL) to inhibit fungal and bacterial contamination respectively. Plates were incubated at 28 °C for 28 days. The colonies were purified by consecutive reseed on ISP2 agar and preserved in a spore solution with 50% glycerol at – 80 °C.

Morphological Characterization of Isolated *Streptomyces* species

Phenotypic identification of purified isolates was based on culture and morphological characteristics using standard methods described in the International *Streptomyces* Project [30]. The morphological determinations included aerial mycelium and substrate coloration, soluble pigment production, colony texture and Gram staining.

Qualitative Determination of Enzymatic Activity

The ability of the isolated strains to produce Endoglucanases (CMCase) and Xylanase (Xyl) activity during their growth on plate was determined. For the detection of CMCase activity Agar plates [31] were used with the following composition: carboxymethylcellulose (CMC) 2.0 g/L, $(NH_4)_2SO_4$ 0.5 g/L, $CaCl_2$ 0.1 g/L, K_2HPO_4 1 g/L, $MgSO_4$ 0.2 g L, KCl 0.5 g/L, yeast extract (Dibico) 0.5 g/L and bacteriological agar (Dibico)18 g/L at pH 7.0. After the incubation period (10 days at 28 °C), the plates were stained with lugol-iodine solution for 10 min, the solution was removed and rested for 1 h. The plates with cellulolytic activity showed clear areas around the colony [32]. Whereas, for the detection of Xyl activity, xylan agar [33] was used with the following composition: birch xylan 2 g L, $(NH_4)_2SO_4$ 0.5 g/L, $CaCl_2$ 0.1 g/L, K_2HPO_4 1 g/L, $MgSO_4$ 0.2 g/L, KCl 0.5 g/L, yeast extract (Dibico) 0.5 g/L, peptone 0.0015 g/L and bacteriological agar (Dibico) 20 g/L at pH 7.0. The plates were incubated 10 days at 28 °C and subsequently stained with Congo red solution (0.2%) for 10 min and consecutive washes with 1 M NaCl solution. The plates with positive Xyl activity showed yellow areas against red bottoms [34]. The results were reported indicating the radius of the hydrolysis zones and were classified as: (+) weak producer (0.8–1.4 cm); (++) moderate producer (1.5–2.4 mm) and (+++) strong producer (2.5–3.0 mm) [35]. All chemical reagents from tha basal medium were purchased from Sigma-Aldrich.

Raw Material

The barley straw was washed with tap water, dried at 60 °C for 12 h in a convection oven (Thermo Scientific), then cut in lengths of 5 cm, ground in a commercial grain mill (Thomas Scientific) and passed through sieves Inox mesh size 8 (2380 μm) and 12 (1680 μm). Finally, the ground straw was stored in airtight containers.

Inoculum Preparation

Each *Streptomyces* specie was grown on ISP2 agar plates until sporulation at 28 °C. For the spore harvest, 5 mL of sterile distilled water was added per plate and with the help of a sterile disposable spatula the mycelium spores were detached. The resulting solution was stored under refrigeration (4 °C) and the spore count was performed with a Neubauer chamber (Marienfeld).

Solid-State Cultivation (SSC)

The SSC was carried out in 250 mL Erlenmeyer flasks, 1 g of barley straw was added to each flask and both autoclaved at 121 °C for 15 min. Particle sizes of 1680 and 2380 μm were evaluated in independent experiments. Under aseptic conditions, 1×10^7 spores/gdm (grams of dry mater) of each *Streptomyces* specie was added to each flask and incubated at 28 °C, the humidity was adjusted to 85% with sterile distilled water. A 10-day kinetics (240 h) was carried out for the quantification of the enzymatic activities of CMCase and Xyl in liquid, samples were taken in triplicate every 24 h from which the crude enzyme extract was obtained. To obtain the crude extract, 20 mL of acetate buffer (100 mM, pH 5.3) was added to each flask and stirred at room temperature for 20 min at 180 rpm. The extract was centrifuged for 10 min at 10,000 rpm at 4 °C and was received in tubes (50 mL) and kept at 4 °C until further analysis.

Quantitative Determination of Enzymatic Activity

CMCase and Xyl activity was estimated from the release of reducing sugars by the DNS method [36]. Enzymatic extracts were incubated for 20 min at 40 °C in a reaction mixture with CMC or birch xylan (0.2% w/v in 100 mM acetates buffer, pH 5.3) according to Loera and Cordova [37]. The standard curve was performed with glucose or xylose at a concentration of 2 mg/mL. One unit of enzymatic activity was defined as the amount of enzyme needed to release 1 μmoL of glucose or xylose per minute under the conditions tested. The protein concentration in the supernatants was determined according to the method of Bradford [38], using bovine serum albumin as standard. All analysis was performed in triplicate and the average rates were calculated to represent enzyme activity.

Molecular Identification

The *Streptomyces* species were identified based on the sequencing of the 16S rDNA gene. For DNA extraction,

biomass was obtained from culturing the strains in ISP2 liquid medium at 28 °C for 48 h and 150 rpm. Total genomic DNA was extracted according to the CTAB procedure [39] (Wilson, 1997). The 16S rDNA gene was amplified by PCR using primers 8F (5′-AGAGTTTGA TCCTGGCTCAG-3′) and 1492R (5′-GGTTACCTTGTT ACGACTT-3′) in a thermocycler (SimpliAmp, Applied Biosystems, California, USA). The PCR amplification of 10 ng of genomic DNA was carried out in a volume of 25 µL of reaction, the composition of the reaction mixture was: 1 × Taq Buffer (10 mM Tris–HCl, 50 mM KCl, pH 8.3), $MgCl_2$ 2.5 mM, 200 µM dNTP's, 0.4 µM of each primer and 1 U Taq DNA polymerase. The PCR program consisted of an initial denaturation of 94 °C for 3 min, 25 cycles of denaturation (94 °C for 30 s), alignment (53 °C for 30 s), extension (72 °C for 1 min 40 s) and final extension at 72 °C for 10 min. In both cases, the integrity of the DNA as well as the size of the amplified bands were determined by 1% agarose gel horizontal electrophoresis that were revealed with ethidium bromide (0.5 µg/mL) and visualized with ultraviolet light (254 nm). The PCR products were purified with the Wizard® SV Gel and PCR Clean-Up System kit (Promega, USA), taking into account the instructions suggested by the supplier and sequenced in a 16-capillary automatic sequencer (Applied Biosystems, model 3130xl) at the facilities of the Synthesis and Sequencing Unit of the Biotechnology Institute of the UNAM (Morelos, Mexico).

The ribosomal gen16s sequences were manually edited based on the quality of the electropherograms using the Chromas v2.6.6 software (https://technelysium.com.au). The degree of similarity with other closest sequences deposited in the GenBank (https://www.nlm.nih.gov/) was determined by BLAST (Basic Local Alignment Search Tool) program. The sequences were aligned with reference actinomycete strains in the CLUSTAL × 2.1 program (https://www.clustal.org/clustal2/) [40] and edited in BioEdit Sequence Alignment Editor [41]. All the sequences were deposited in the GenBank. The phylogenetic tree was constructed using the Bayesian inference method by means of BEAST v1.8.4 software and the General Time-Reversible Nucleotide Substitution Model (GTR) [42] obtained through the jModelTest v2.1.10 program [43] based on the Akaike Information Criterion (AIC), with a bootstrap value of 1000 replicas. The graphic representation and edition of the phylogenetic tree was done in FigTree version 1.4.3 (https://tree.bio.ed.ac.uk/software/figtree/). The genera *Nocardia asteroides* ATCC 19247 and *Micromonospora echinospora* ATCC 15837 were chosen because of their close phylogenetic relationship with the genus *Streptomyces*, while *Bacillus circulans* subsp. ATCC 4513 circulans was used as an external group.

Statistical Analysis

For the analysis of variance (ANOVA) and comparison of means by the Tukey method OriginPro 8 software (OriginLab Corporation, Northampton, Massachusetts, USA) and Minitab 17 (Minitab Inc., State College, PA, USA) respectively were used.

Results and Discussions

Isolation of *Streptomyces* Species

In this first stage 73 possible *Streptomyces* species were isolated from the two-soil rhizosphere of the MV, based on morphological and growth characteristics. Of the total isolates, 42.47% were obtained in ISP2 agar and 57.53% in ISP3 agar. The most suitable medium for the isolation of *Streptomyces* species in this study was ISP3, which according to the International *Streptomyces* Project is recognized as one of the most effective medium of obtaining high proportions of actinomycetes [30].

There is a great variation in the number of actinomycetes recovered from the rhizosphere, studies such as that of Hozzein et al. [44], report the isolation of 27 actinomycetes from soils in the Jouf region, Saudi Arabia using yeast extract agar and glycerol, while Salehghamari et al. [45] they isolated 69 actinomycetes in Alborz soil, Iran, on yeast extract agar plates-malt extract and casein starch agar. The differences found in the number of isolates are related to the different media and generally to the nutrient content in each of them and to the requirements on the part of the microorganisms, however, the actinomycetes present nutritional versatility which makes them be present in a large number of environments [46]. The diversity of the microorganisms present in the rhizosphere is correlated with the level of organic matter in soils [47]. The MV, receiving untreated wastewater effluents for irrigation, allows the incorporation of water, nitrogen, phosphorus, nutrients and low molecular weight organic compounds that can be used by soil biota [48, 49], it has been described that prolonged use of wastewater has a great effect on soil microbial communities [50]. Lüneberg et al. [26], reported 45 bacterial species in soils of the MV, being the predominant the actinobacteria with 30% of the total microbial communities. However, different results have been reported indicating that wastewater contains high concentrations of salt that increase soil salinization, with the consequent decrease in microbial biomass and enzymatic activities [51].

Fig. 1 Hydrolysis halo formed around an actinomycete colony. **A** 0.2% CMC agar stained with lugol-iodine solution for Endoglucanase activity; **B** 0.2% xylan agar stained with Congo red solution and 1 M NaCl washes for xylanase activity

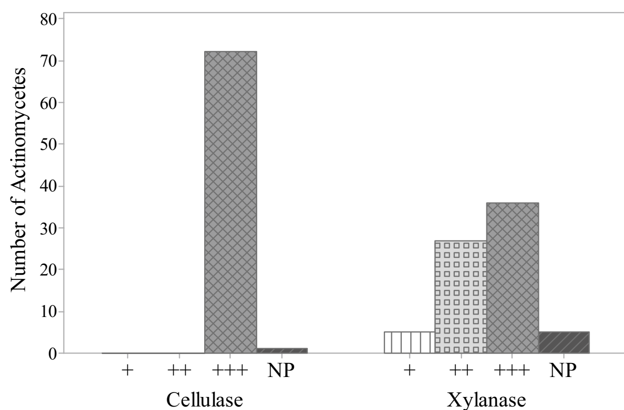


Fig. 2 Production of CMCase and Xyl of *Streptomyces* species (72 strain) grown on plate with 0.2% CMC and 0.2% birch xylan as substrates for 10 days at 28 °C. *NP* no activity, + weak producer (halo 0.8–1.4 mm), ++ moderate producer (halo 1.5–2.4 mm), +++ strong producer (halo 2.5–3.0 mm)

Qualitative Enzymatic Determination

All strains were evaluated for their ability to produce CMCase and Xyl extracellular enzymes using specific colorimetric staining methods for each of the enzymatic activities sought. The interactions between dye-polysaccharide provide a visual indication of the hydrolysis of the substrate reflected in clear areas or halos around the growth colony (Fig. 1) [52].

Of the 73 isolates, 72 strains (98.63%) showed positive activity for CMCase production in CMC agar plates stained with lugol-iodine solution (Fig. 2). Several studies report that lugol-iodine solution staining is an easy and fast method to detect microorganisms producing lignocellulolytic enzymes mainly identifying as endoglucanases, in addition to generating a strong increase in the color contrast of the hydrolyzed area and the non-hydrolyzed portion [53, 54]. On the other hand, 68 isolates (93.15%) were positive for Xyl using as birch xylan substrate stained with Congo red solution (Fig. 2). Congo red interacts with 1,4-β-D-glucans, 1,3-β- D-glucans and 1,4-β- D-xylanes [55], which makes it the dye more using in the detection of Xyl in plate [56].

Of the strains studied, 72 showed to be strong CMCase producers (+++) and only one did not show this activity. Regarding the xylanolytic activity, 35 strains showed to be strong producers of xylanase (+++), 28 strains were moderate producers of xylanase (++), 5 strains were weak producers of xylanase (+) and five did not show this activity (Fig. 2) according to the scale of Porsuk et al. [32]. For the next stage that was the SSC, 38 strains were chosen, which were the ones that presented, on average, the highest halo of enzymatic activity for both CMCase and Xyl.

Quantitative Enzyme Activity of Crude Enzyme Extracts

SSC is a growth process in which microorganisms are able to grow in solid media that have relatively low water activity, which is trapped between the structure of the substrate in the form of free water.[57]. The microorganisms more viable to grow in solid medium are filamentous fungi, although actinomycetes such as *Streptomyces* sp. they are also able to grow in SSC systems, since they have characteristics such as abundant solid waste colonization, production of a wide range of hydrolytic enzymes and high resistance to extreme conditions [58].

SSC technology used by its importance for the generation of products with high added value, for example, enzymes from agro-industrial by-products [59]. The CMCase and Xyl production by the 38 *Streptomyces* species in SSC over a period of 240 h is observed in Fig. 3. The values indicated in the graph belong to the maximum enzymatic synthesis on barley straw with a particle size of 1680 µm. The growth of microorganisms on the substrate was evident this suggests that barley straw is used as a substrate promoting the expression of CMCase and Xyl during the growth of the microorganisms used.

The CMCase activity of the 38 strains of actinomycetes and the day of maximum production is shown in Table 1. The strain 15 was the one that showed the highest cellulolytic activity with 26.02 AU/gdm at 192 h of incubation. The behavior in the production of CMCase enzymes in SSC systems was very heterogeneous and showed no tendency during the respective kinetics, this same behavior was observed when determining the xylanolytic activity where strain 30 was the one that produced the high more xylanolytic activity with 100.65 AU/gdm at 216 h of incubation (Table 1).

The behavior of the strains is interesting, where a greater xylanolytic activity is observed in comparison with the cellulolytic activity. The greater Xyl activity is probably due to the structure of the plant material itself, since structurally,

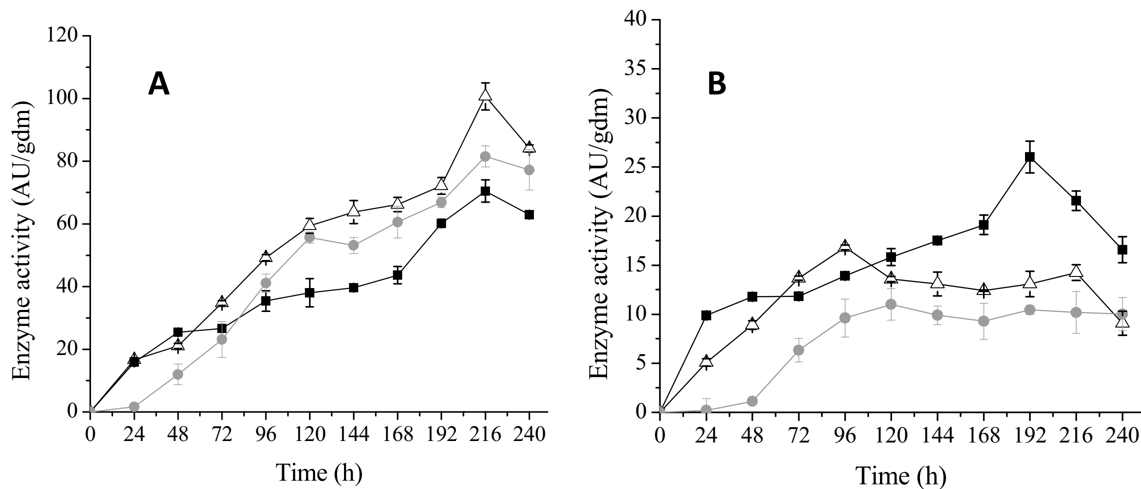


Fig. 3 Enzymatic profile of *Streptomyces* species, strain 15 (filled square), strain 28 (filled circle) and strain 30 (open triangle) using barley straw with particle size 12 (1680 µm) as a substrate in SSF for a period of 240 h. **A** Xylanolytic activity, **B** CMCase activity

hemicellulose (like xylan) is more exposed, and therefore, it is the polymer that is first degraded.

Longer fermentation times may favor CMCase production; this may be due to the need for a previous Xyl action to expose the cellulose fibers, which will induce the production of cellulases [60]. In addition, it has been reported that the presence of hemicelluloses, xylooligosaccharides and cellobiose in the fermentation medium has an inhibitory effect on the cellulolytic hydrolysis of biomass [61, 62], reason that could justify the low yields obtained for CMCases.

The studies carried out of the production of CMCase and Xyl enzymes in plate and SSC allowed selecting the three strains that presented the highest enzymatic activities. The chosen strains presented both enzymatic activities but in different proportions, in general, the xylanolytic activity was greater than the cellulolytic activity. The production of CMCase and Xyl of the strains using the barley straw as the only carbon source is shown in Fig. 3. Enzyme production increased gradually during the fermentation period, for Xyl activity the maximum values were obtained by strain 30 (100.69 AU/gdm), followed by strain 28 (81.53 AU/gdm) and strain15 (70.47 AU/gdm), at 216 h of incubation (Fig. 3a). The maximum production of cellulolytic activity was observed with strain 15 (26.02 AU/gdm) at 196 h of incubation (Fig. 3b).

In addition, the particle size of 2380 µm was evaluated in order to determine which particle promotes an increase in enzyme production. The results obtained in the production of the hydrolytic enzymes for strains 15, 28 and 30 are shown in Fig. 4, it is observed that for the enzymatic activities of CMCase and Xyl in the first hours of growth there is an increase in catalytic activity, subsequently there is a decay in the enzymatic activity, probably due to factors associated with the decrease of space for growth or depletion of nutrients. For strain 30 the maximum activities of CMCase (15.06 AU/gdm) and Xyl (78.09 AU/gdm) were detected at 240 and 216 h of incubation, respectively. The maximum catalytic activities for strains 15 and 28 were 61.76 and 67.13 AU/gdm of Xyl (120 and 168 h) and 25.73 and 11.47 AU/gdm of CMCase (216 and 192 h), respectively.

Of the two particle sizes studied, the 1680 µm particle favored the production of Xyl and CMCase due to the increase in the surface area of the substrate. Small particle sizes of lignocellulosic material increase the exposure of cellulose and hemicellulose compartments which benefits microbial binding [63]. Meanwhile, the 2380 µm particle provided larger spaces between the substrate, which generated better conditions for heat and mass transfer, but decreased the surface area for actinomycetes [64].

Most of what is reported by other authors regarding the enzymatic activities of CMCase and Xyl by actinomycetes are in the submerged fermentation (SmF) preferably, because it is possible to control the degree of aeration, agitation, pH, temperature, foam and other environmental factors for better process control [65]. The genus *Streptomyces* is the most studied in SmF [66–70]. Regarding the SSC, agroindustrial substrates are used as supports for the production of enzymes, Srivastava [71] studied a strain of *Thermomonospora* 29 in the presence of coffee residues supplemented with mineral salts were arabinosidases, Xyl and β-D-xylosidases production was studied. Beg et al. [72], reported the culture of *Streptomyces* sp. QG-11–3 in wheat bran and eucalyptus kraft pulp for the production of a thermostable Xyl enzyme. Similarly, Bajaj and Singh [73] used a strain of *Streptomyces* sp. 7b grown in wheat bran pretreated with steam to detect Xyl and Singh et al. [74], mixed rice bran and wheat in the presence of *Streptomyces* sp. MSC702 to evaluate amylases and Xyl production.

Table 1 Hydrolytic enzymes production (cellulases and xylanases) of streptomycetes isolated from agricultural soils, indicating the time when the maximum enzymatic activity was detected

Strain	Cellulase (AU/gdm)	Maximun production time (hours)	Xylanase (AU/gdm)	Maximun production time (hours)
1	13.58 ± 0.46	168	47.28 ± 0.99	144
2	13.54 ± 0.51	216	45.81 ± 0.77	72
3	13.66 ± 0.37	96	31.32 ± 1.09	72
4	11.04 ± 0.46	168	47.55 ± 0,49	168
5	17.51 ± 0.55	144	32.41 ± 0.41	48
6	12.15 ± 0.68	168	19.89 ± 0.41	72
7	6.85 ± 0.25	168	23.16 ± 0.74	216
8	13.58 ± 0.07	96	60.13 ± 0.86	240
9	12.07 ± 0.19	96	31.34 ± 0.77	240
10	18.29 ± 1.29	168	63.12 ± 0.66	96
11	3.10 ± 0.26	216	14.45 ± 0.74	144
12	5.06 ± 0.44	72	24.79 ± 0.82	120
13	10.23 ± 0.39	168	24.41 ± 0.84	168
14	3.90 ± 0.43	240	13.36 ± 0.66	240
15	26.02 ± 0.61	192	70.47 ± 1.57	216
16	11.05 ± 0.96	216	26.42 ± 0.74	240
17	12.19 ± 1.49	240	59.75 ± 1.34	96
18	14.81 ± 0.68	168	48.80 ± 1.43	120
19	11.17 ± 0.12	168	36.28 ± 1.07	168
20	18.82 ± 1.11	168	56.21 ± 0.75	216
21	13.05 ± 0.26	240	35.30 ± 0.71	144
22	5.51 ± 1.39	144	16.24 ± 0.25	144
23	8.11 ± 1.43	192	14.71 ± 0.47	120
24	8.55 ± 0.96	192	19.13 ± 0.86	120
25	13.62 ± 0.68	96	32.84 ± 0.99	96
26	14.28 ± 0.68	144	25.50 ± 0.75	144
27	19.92 ± 0.80	168	21.80 ± 0.53	168
28	11.01 ± 1.31	120	81.53 ± 0.43	240
29	20.66 ± 0.51	96	36.33 ± 0.66	96
30	16.81 ± 0.26	96	100.69 ± 0.99	216
31	9.09 ± 0.14	144	39.38 ± 0.75	144
32	5.96 ± 0.31	120	23.10 ± 0.34	240
33	12.31 ± 0.26	120	36.77 ± 0.33	120
34	12.01 ± 2.51	216	55.77 ± 1.76	96
35	14.89 ± 1.31	192	59.26 ± 1.34	192
36	12.03 ± 0.32	72	56.10 ± 0.68	216
37	15.42 ± 0.50	192	35.46 ± 0.91	192
38	11.78 ± 0.37	96	31.32 ± 1.23	120

Postharvest agricultural waste is an inedible fraction of food crops or the plant [75], its use as substrate for the production of enzymes is a way of substantially reducing the total cost of the agricultural processes [76]. In this study it has been shown that barley straw is an interesting material to be used as a substrate for the production of enzymes. In addition to its low economic cost, is has wide availability and a low impact on food production. Straw is the most common organic waste, usually used as feed for cattle, but due to its low digestibility it is often abandoned, or it is incinerated resulting in serious environmental problems [77, 78].

Morphological and Molecular Identification of Streptomyces Species Producing CMCase and Xyl

The macroscopic characteristics of isolates 15, 28 and 30 selected for their potential to produce Xyl and CMCase were observed for 10 days in ISP2 medium (Table 2) Colony 15 showed light gray aerial mycelium, with production

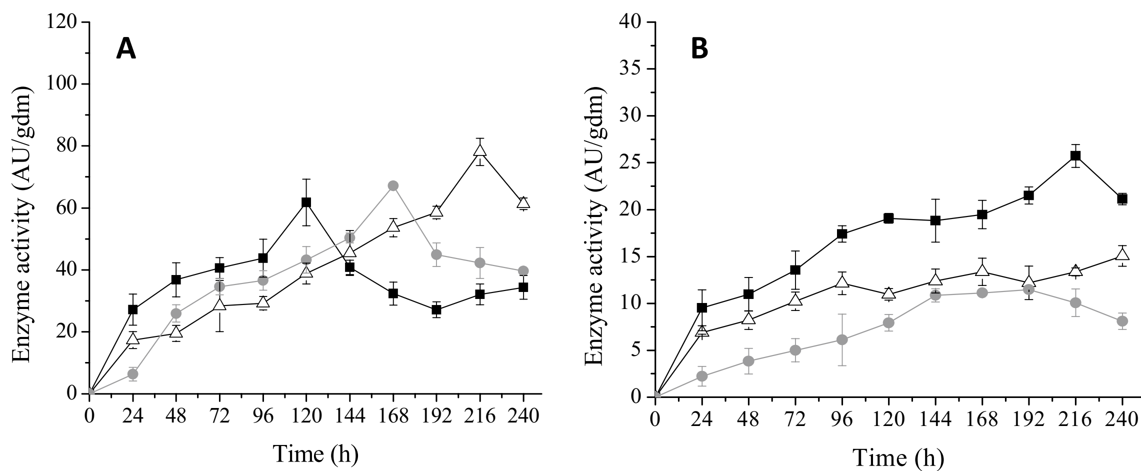


Fig. 4 Enzymatic profile of *Streptomyces* species 15 (filled square), 28 (filled circle) and 30 (open triangle) using barley straw with particle size 8 (2380 µm) as a substrate in SSF for a period of 240 h. **A** Xylanolytic activity, **B** CMCase activity

Table 2 Morphological identification of the actinomycete strains on ISP2 agar for 10 days at 28 °C. A) Strain 15; B) Strain 28; C) Strain 30

Strain	Growth type	Mycelium	Mycelium aerial	soluble pigments	Gram staining
15	Moderate	Gray-White	Brown	Yellow	+
28	Abundant	Pink-Whitre	Brown	–	+
30	Moderate	Gray	Red	Red	+

of diffusible exopigments to the medium of yellow hue at 6 days. The colony 28 was initially white and opaque since it did not produce any soluble pigment, after 5 days the presence of abundant aerial hyphae was evident that turned the plate pink. In contrast, the colony 30 exhibited light to dark gray aerial mycelium with red exopigment secretion at 7 days. The 3 strains showed a dry, powdery texture and adhered to the substrate, also proved to be Gram positive, typical characteristic of these microorganisms.

Molecular identification was performed by sequencing the ribosomal gen16s. Nucleotide similarity search analysis in BLAST revealed that the isolates are closely related to the genus *Streptomyces*. The phylogenetic analysis included sequences of external strains that indicated that the closest species for strain 15 was *Streptomyces flavogriseus* with 100% similarity (GenBank accession number MN581662), strain 28 was related to *Streptomyces virginiae* with 99.89% (GenBank accession number MN581663) of similarity and strain 30 with *Streptomyces griseoaurantiacus* with 99.89% (GenBank accession number MN581664) of similarity as shown in the phylogenetic tree of Fig. 5. It has been previously described to *S. flavogriseus* for its capacity to produce high levels of extracellular enzymes capable of hydrolyzing cellulose and xylan, the main enzymes described in this microorganism are: xylanases [79], exoglucanases [80], cellulases and glucose isomerases [81, 82]. There are few studies of microorganisms that produce cellulolytic activity, however *S. flavogriseus* is particularly interesting because it has hemicellulose de-branching enzymatic activities for the most efficient degradation of lignocellulosic biomass [83]. More recently, Pennacchio et al. [84], formulated a mixture with xylanase and cellulase activity of two strains of *S. flavogriseus* AE64X and AE63X for use in saccharification of pretreated lignocellulose, obtaining yields of up to 86%. In the case of *S. griseoaurantiacus*, Chu et al. [85] they isolated strains that grew on amorphous cellulose (carboxymethyl cellulose) and produced endoglucanases at pH 5.0 and 50 °C, in addition to hydrolyzing purified bamboo cellulose with the secretion of β-glucosidases. Like, Kumar [86] they build two mutants of *S. griseoaurantiacus* with improved activities of endoglucanase and β-glucosidase highly thermostable at 80 °C and tested them in rice straw as the only carbon source. The present study confirms to *S. flavogriseus* and *S. griseoaurantiacus* as producers of CMCase and Xyl through the degradation of lignocellulosic residues.

Meanwhile for *S. virginiae*, Iizuka and Kawaminami [87] and Macagnan et al. [88] indicated that the species is not capable of producing cellulases, β-1, 3-glucanases and xylanases when using simple substrates, because this type of compounds were not capable of inducing the synthesis of enzymes. The

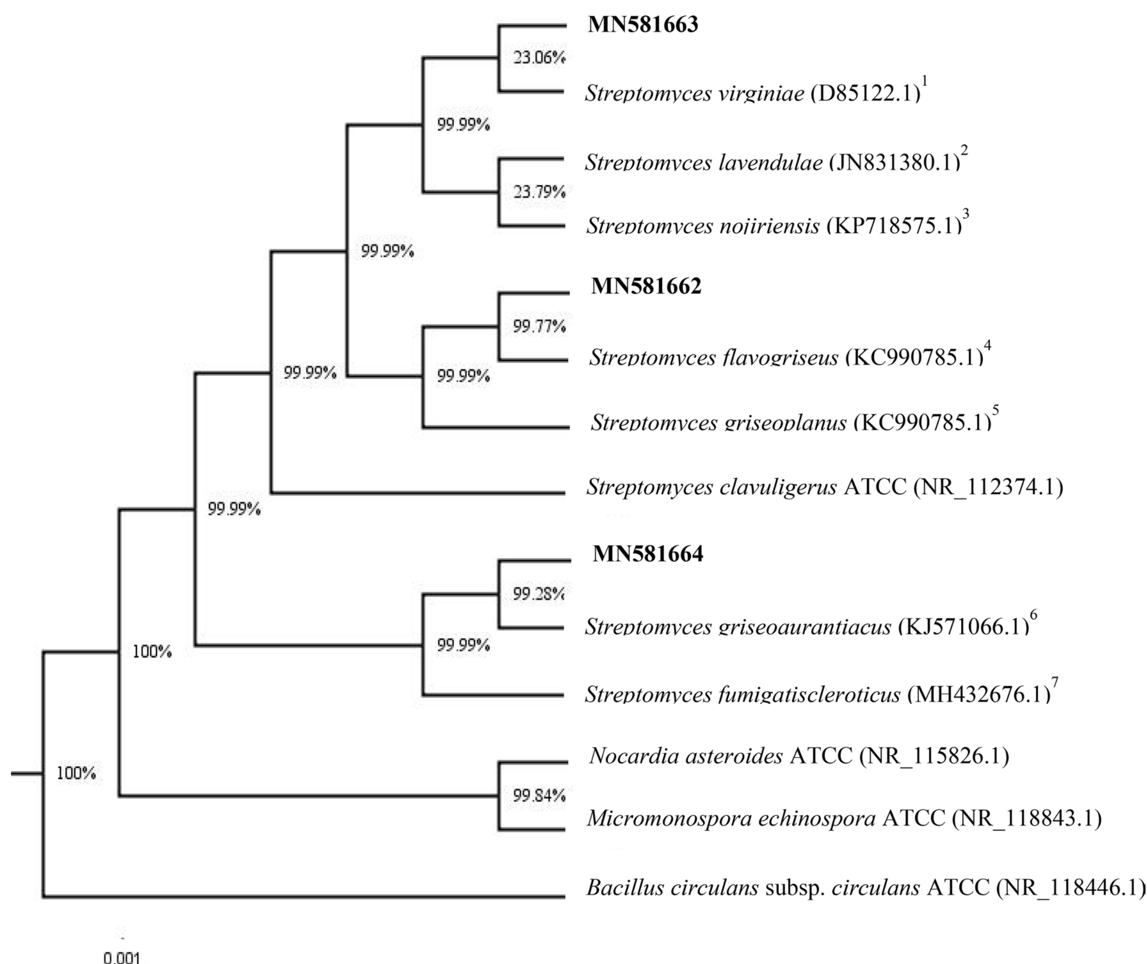


Fig. 5 Phylogenetic tree of *Streptomyces* species selected for their enzymatic potential built with the GenBank code number of each of the strains. Evolutionary relationships based on ribosomal gen 16S sequence alignments are shown. The numbers in the nodes indicate the similarity percentages. The bar indicates 0.001 substitutions per nucleotides position. Strain 15 (*Streptomyces flavogriseus*, GenBank code number MN581662); strain 28 (*Streptomyces virginiae*, GenBank code number MN581663); strain 30 (*Streptomyces griseoaurantiacus*, GenBank code number MN581664); [1][89]; [2][90]; [3][91]; [4][92]; [5][93]; [6][94]; [7][95]

availability of nutrients is more restricted in solid substrates than in liquid cultures, due to the fact that in a liquid state there is more availability of nutrients since they are part of the solution, a situation that does not happen in solid substrates since generally (as in the case of plant matter) they are part of the structure. For microorganisms to have access to substrates, they must first be able to hydrolyze them, therefore it is necessary to develop more efficient enzyme systems for degradation of the solid residuals, so it is suggested that *S. virginiae* was able to produce CMCase and Xyl in presence of a complex substrate such as barley straw, this being the first report of its enzymatic potential.

Conclusions

In this study, *Streptomyces* species isolated from semi-arid areas of the MV demonstrated high cellulolytic (endoglucanase) and xylanolytic productivity by using barley straw as the sole substrate in solid-state fermentation. Under the conditions tested in this work, the particle size of 1680 µm favored greater catalytic activity for *S. flavogriseus*, *S. virginiae* and *S. griseoaurantiacus* strains. This study presented the first report of the production of hydrolytic enzymes by *S. virginiae*.

Acknowledgements This work was carried out with the support received by the National Council of Science and Technology (CONACyT) with registration 557540 and to the PhD scholarship awarded by ConacyT No. 467187. The authors are grateful to Ing. Jaime Ortega Bernal for providing access to the experimental platform of Cinta Larga, Mixquiahuala, Hidalgo.

Author contributions YEC: Methodology, Validation, Formal analysis, Writing-original draft. YM: Validation, Data curation, Visualization. MAA: Software, Formal analysis, Validation. JÁ: Methodology, Investigation. BP: Term, Conceptualization, Methodology, Visualization. ZE: Term, Methodology, Visualization, Investigation. AT: Term, Conceptualization, Writing-Review & Editing, Supervision, Funding acquisition.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

References

1. Das S, Lyla PS, Khan SA (2008) Distribution and generic composition of culturable marine actinomycetes from the sediments of Indian continental slope of Bay of Bengal. Chin J Oceanol Limnol 26(2):166–177. https://doi.org/10.1007/s00343-008-0166-5
2. Bhatti AA, Haq S, Bhat RA (2017) Actinomycetes benefaction role in soil and plant health. Micro Pathog 111:458–467. https://doi.org/10.1016/j.micpath.2017.09.036
3. Bhakyashree K, Kannabiran K (2018) Actinomycetes mediated targeting of drug resistant MRSA pathogens. J King Saud Univ Sci. https://doi.org/10.1016/j.jksus.2018.04.034
4. Messaoudi O, Bendahou M, Benamar I, Abdelwouhid DE (2015) Identification and preliminary characterization of non-polyene antibiotics secreted by new strain of actinomycete isolated from sebkha of Kenadsa, Algeria. Asian Pac J Trop Biomed 5(6):438–445. https://doi.org/10.1016/j.apjtb.2015.04.002
5. Benhadj M, Gacemi-Kirane D, Menasria T, Guebla K, Ahmane Z (2018) Screening of rare actinomycetes isolated from natural wetland ecosystem (Fetzara Lake, northeastern Algeria) for hydrolytic enzymes and antimicrobial activities. J King Saud Univ Sci. https://doi.org/10.1016/j.jksus.2018.03.008
6. Ouchari L, Boukeskasse A, Bouizgarne B, Ouhdouch Y (2019) Antimicrobial potential of actinomycetes isolated from the unexplored hot Merzouga desert and their taxonomic diversity. Biology Open 8(2):bio035410. https://doi.org/10.1242/bio.035410
7. Abdelmohsen UR, Grkovic T, Balasubramanian S, Kamel MS, Quinn RJ, Hentschel U (2015) Elicitation of secondary metabolism in actinomycetes. Biotechnol Adv 33(6):798–811. https://doi.org/10.1016/j.biotechadv.2015.06.003
8. Atta HM (2015) Biochemical studies on antibiotic production from *Streptomyces* sp.: taxonomy, fermentation, isolation and biological properties. J Saudi Chem Soc 19:12–22. https://doi.org/10.1016/j.jscs.2011.12.011
9. Weber T, Charusanti P, Musiol-Kroll EM, Jiang X, Tong Y, Kim HU, Lee SY (2015) Metabolic engineering of antibiotic factories: new tools for antibiotic production in actinomycetes. Trends Biotechnol 33(1):15–26
10. Mohan GM, Charya MAS (2012) Enzymatic activity of fresh water actinomycetes. Int Res J Pharm 3:193–197. https://doi.org/10.1016/j.tibtech.2014.10.009
11. Choi SS, Kim HJ, Lee HS, Kim P, Kim ES (2015) Genome mining of rare actinomycetes and cryptic pathway awakening. Process Biochem 50(8):1184–1193. https://doi.org/10.1016/j.procbio.2015.04.008
12. Varalakshmi T, Sekhar KM, Charyulu PBB (2014) Taxonomic studies and phylogenetic characterization of potential and pigmented antibiotic producing actinomycetes isolated from rhizosphere soils. Int J Pharm Pharm Sci 6(6):511–519
13. Shah AM, Rehman S, Hussain A, Mushtaq S, Rather MA, Shah A, Ahmad Z, Khan IA, Bhat KA, Hassan QP (2017) Antmicrobial investigation of selected soil actinomycetes isolated from unexplored regions of Kashmir Himalayas, India. Microb Pathog 110:93–99. https://doi.org/10.1016/j.micpath.2017.06.017
14. Mohammadipanah F, Wink J (2016) Actinobacteria from arid and desert habitats: diversity and biological activity. Front Microbiol 6:1541. https://doi.org/10.3389/fmicb.2015.01541
15. Vieille C, Zeikus GJ (2001) Hyperthermophilic enzymes: sources, uses, and molecular mechanisms for thermostability. Microbiol Mol Biol Rev 65(1):1–43. https://doi.org/10.1128/MMBR.65.1.1-43.2001
16. Bennur T, Kumar AR, Zinjarde S, Javdekar V (2015) Nocardiopsis species: incidence, ecological roles and adaptations. Microbiol Res 174:33–47. https://doi.org/10.1016/j.micres.2015.03.010
17. Johri JK, Surange S, Nautiyal CS (1999) Occurrence of salt, pH, and temperature-tolerant, phosphate-solubilizing bacteria in alkaline soils. Curr Microbiol 39(2):89–93. https://doi.org/10.1007/s002849900424
18. Gurovic MSV, Olivera NL (2017) Antibacterial producing actinomycetes from extra Andean Patagonia. J Arid Environ 144:216–219. https://doi.org/10.1016/j.jaridenv.2017.04.015
19. Aouar L, Lerat S, Ouffroukh A, Boulahrouf A, Beaulieu C (2012) Taxonomic identification of rhizospheric actinobacteria isolated from Algerian semi-arid soil exhibiting antagonistic activities against plant fungal pathogens. Can J Plant Pathol 34(2):165–176. https://doi.org/10.1080/07060661.2012.681396
20. Korayem AS, Abdelhafez AA, Zaki MM, Saleh EA (2015) Optimization of biosurfactant production by *Streptomyces* isolated from Egyptian arid soil using Plackett-Burman design. Ann Agric Sci 60(2):209–217. https://doi.org/10.1016/j.aoas.2015.09.001
21. Yeager CM, Gallegos-Graves LV, Dunbar J, Hesse CN, Daligault H, Kuske CR (2017) Polysaccharide degradation capability of *Actinomycetales* soil isolates from a semiarid grassland of the Colorado Plateau. Appl Environ Microbiol 83(6):e03020–e3116. https://doi.org/10.1128/aem.03020-16
22. González-Méndez B, Webster R, Fiedler S, Loza-Reyes E, Hernández JM, Ruíz-Suárez LG, Siebe C (2015) Short-term emissions of CO_2 and N_2O in response to periodic flood irrigation with waste water in the Mezquital Valley of Mexico. Atmos Environ 101:116–124. https://doi.org/10.1016/j.atmosenv.2014.10.048
23. Sánchez-González A, Chapela-Lara M, Germán-Venegas E, Fuentes-García R, del Río-Portilla F, Siebe C (2017) Changes in quality and quantity of soil organic matter stocks resulting from wastewater irrigation in formerly forested land. Geoderma 306:99–107. https://doi.org/10.1016/j.geoderma.2017.07.009
24. Montelongo-Reyes MM, Otazo-Sánchez EM, Romo-Gómez C, Gordillo-Martínez AJ, Galindo-Castillo E (2015) GHG and black carbon emission inventories from Mezquital Valley: the main energy provider for Mexico Megacity. Sci Total Environ 527:455–464. https://doi.org/10.1016/j.scitotenv.2015.03.129
25. Broszat M, Nacke H, Blasi R, Siebe C, Huebner J, Daniel R, Grohmann E (2014) Wastewater irrigation increases abundance of potentially harmful *Gammaproteobacteria* in soils from Mezquital Valley, Mexico. Appl Environ Microbiol 80(17):5282–5291. https://doi.org/10.1128/AEM.01295-14
26. Lüneberg K, Schneider D, Siebe C, Daniel R (2018) Drylands soil bacterial community is affected by land use change and different irrigation practices in the Mezquital Valley, México. Sci Rep 8(1):1413. https://doi.org/10.1038/s41598-018-19743-x

27. Diario Oficial de la Federación. Norma Oficial Mexicana: NOM 021-SEMARNAT-2000 (2002) Que establece las especificaciones de fertilidad, salinidad y clasificación de suelos. Estudios, muestreo y análisis. México
28. Hayakawa M (2008) Studies on the isolation and distribution of rare actinomycetes in soil. Actinomycetologica 22:12–19. https://doi.org/10.3209/saj.SAJ220103
29. Oskay AM, Üsame T, Cem A (2004) Antibacterial activity of some actinomycetes isolated from farming soils of Turkey. Afr J Biotechnol 3(9):441–446. https://doi.org/10.5897/AJB2004.000-2087
30. Shirling EB, Gottlieb D (1966) Method for characterization of *Streptomyces* species. Int J Syst Bacteriol 16(3):313–340
31. Malisorn K, Nikhome K (2014) Isolation and screening of actinomycetes from soil for their enzymatic and antifungal activity. Khon Kaen Agric J 42(4):151–156
32. Jaralla EM, Al-Dabbagh NN, Hameed N, Abdul-Hussain N (2014) Screening for enzymatic production ability and antimicrobial activity of actinomycetes isolated from soil in Hillah/Iraq. J Pharm Biol Sci 9:42–47
33. Nakamura S, Wakabayashi K, Nakai R, Aono R, Horikoshi K (1993) Purification and some properties of an alkaline xylanase from alkaliphilic *Bacillus* sp. strain 41 M-1. Appl Environ Microbiol 59(7):2311–2316
34. Abdel-Sater MA, El-Said AHM (2001) Xylan-decomposing fungi and xylanolytic activity in agricultural and industrial wastes. Int Biodeter Biodegr 47(1):15–21. https://doi.org/10.1016/S0964-8305(00)00113-X
35. Porsuk I, Özakin S, Balí B, Yilmaz EI (2013) A cellulase-free, thermoactive, and alkali xylanase production by terrestrial *Streptomyces* sp. CA24. Turk J Biol 37(3):370–375
36. Miller GL, Blum R, Glannon WE, Burton AL (1960) Measurement of carboxymethylcellulase activity. Anal Biochem 1(2):127–132. https://doi.org/10.1016/0003-2697(60)90004-X
37. Loera O, Córdova J (2003) Improvement of xylanase production by a parasexual cross between *Aspergillus niger* strains. Braz Arch Biol Technol 46(2):177–181. https://doi.org/10.1590/S1516-89132003000200000
38. Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal Biochem 72:248–254. https://doi.org/10.1016/0003-2697(76)90527-3
39. Wilson K (2001) Preparation of genomic DNA from bacteria. Curr Prot Mol Biol 56(1):2–4. https://doi.org/10.1002/0471142727.mb0204s56
40. Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res 25:4876–4882. https://doi.org/10.1093/nar/25.24.4876
41. Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp Ser 41:95–98
42. Tavaré S (1986) Some probabilistic and statistical problems in the analysis of DNA sequences. Lect Math Life Sci (Am Math Soc) 17:57–86
43. Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods 9(8):772. https://doi.org/10.1038/nmeth.2109
44. Hozzein WN, Abuelsoud W, Wadaan MAM, Shuikan AM, Selim S, Al Jaouni S, AbdElgawad H (2019) Exploring the potential of actinomycetes in improving soil fertility and grain quality of economically important cereals. Sci Total Environ 651:2787–2798. https://doi.org/10.1016/j.scitotenv.2018.10.048
45. Salehghamari E, Soleimani M, Tafacori V (2015) Antibacterial activity of some actinomycetes isolated from soils of Alborz province Iran. Prog Biol Sci 5(2):159–167
46. Pérez-Corral DA, García-González NY, Gallegos-Morales G, Ruiz-Cisneros MF, Berlanga-Reyes DI, Rios-Velasco C (2015) Isolation of actinomycetes associated to apple trees rhizosphere antagonistic to *Fusarium equiseti*. Rev Mex Cienc Agríc 6(7):1629–1638
47. Khamna S, Yokota A, Peberdy JF, Lumyong S (2009) Actinomycetes isolated from medicinal plant rhizosphere soils: diversity and screening of antifungal compounds, indole-3-acetic acid and siderophore production. World J Microbiol Biotechnol 25(4):649–655. https://doi.org/10.1007/s11274-008-9933-x
48. Friedel JK, Langer T, Siebe C, Stahr K (2000) Effects of long-term waste water irrigation on soil organic matter, soil microbial biomass and its activities in central Mexico. Biol Fert Soils 31:414–421. https://doi.org/10.1007/s003749900188
49. Adrover M, Moyà G, Vadell J (2017) Seasonal and depth variation of soil chemical and biological properties in alfalfa crops irrigated with treated wastewater and saline groundwater. Geoderma 286:54–63. https://doi.org/10.1016/j.geoderma.2016.10.024
50. Hidri Y, Bouziri L, Maron PA, Anane M, Jedidi N, Hassan A, Ranjard L (2010) Soil DNA evidence for altered microbial diversity after long-term application of municipal wastewater. Agron Sustain Dev 30:423–431. https://doi.org/10.1051/agro/2009038
51. Bastida F, Torres IF, Romero-Trigueros C, Baldrian P, Větrovský T, Bayona JM, Alarcón JJ, Hernández T, García C, Nicolás E (2017) Combined effects of reduced irrigation and water quality on the soil microbial community of a citrus orchard under semi-arid conditions. Soil Biol Biochem 104:226–237. https://doi.org/10.1016/j.soilbio.2016.10.024
52. Meddeb-Mouelhi F, Moisan JK, Beauregard M (2014) A comparison of plate assay methods for detecting extracellular cellulase and xylanase activity. Enzyme Microb Technol 66:16–19. https://doi.org/10.1016/j.enzmictec.2014.07.004
53. Kasana RC, Salwan R, Dhar H, Dutt S, Gulati A (2008) A rapid and easy method for the detection of microbial cellulases on agar plates using Gram's iodine. Curr Microbiol 57:503–507. https://doi.org/10.1007/s00284-008-9276-8
54. Guo H, Hong C, Zhang C, Zheng B, Jiang D, Qin W (2018) Bioflocculants production from a cellulase-free xylanase-producing *Pseudomonas boreopolis* G22 by degrading biomass and its application in cost-effective harvest of microalgae. Bioresour Technol 255:171–179. https://doi.org/10.1016/j.biortech.2018.01.082
55. Ruijssenaars HJ, Hartmans S (2001) Plate screening methods for the detection of polysaccharase-producing microorganisms. Appl Microbiol Biotechnol 55:143–149. https://doi.org/10.1007/s002530000477
56. Ping L, Wang M, Yuan X, Cui F, Huang D, Sun W, Zou B, Huo S, Wang H (2018) Production and characterization of a novel acidophilic and thermostable xylanase from *Thermoascus aurantiacus*. Int J Biol Macromol 109:1270–1279. https://doi.org/10.1016/j.ijbiomac.2017.11.130
57. Peng R, He Z, Gou T, Du J, Li H (2019) Detection of parameters in solid state fermentation of *Monascus* by near infrared spectroscopy. Infrared Phys Technol 96:244–250. https://doi.org/10.1016/j.infrared.2018.11.030
58. Soccol CR, da Costa ESF, Letti LAJ, Karp SG, Woiciechowski AL, de Souza Vandenberghe LP (2017) Recent biotechnology research and innovation developments and innovations in solid state fermentation. Biotechnol Res Innov 1(1):52–71. https://doi.org/10.1016/j.biori.2017.01.002
59. Behera SS, Ray RC (2016) Solid state fermentation for production of microbial cellulases: recent advances and improvement strategies. Int J Biol Macromol 86:656–669. https://doi.org/10.1016/j.ijbiomac.2015.10.090

60. Leite P, Salgado JM, Venâncio A, Domínguez JM, Belo I (2016) Ultrasounds pretreatment of olive pomace to improve xylanase and cellulase production by solid-state fermentation. Bioresour Technol 214:737–746. https://doi.org/10.1016/j.biortech.2016.05.028
61. Chen CH, Yao JY, Yang B, Lee HL, Yuan SF, Hsieh HY, Liang PH (2019) Engineer multi-functional cellulase/xylanase/β-glucosidase with improved efficacy to degrade rice straw. Bioresour Technol Rep 5:170–177. https://doi.org/10.1016/j.biteb.2019.01.008
62. Ramamoorthy NK, Sambavi TR, Renganathan S (2019) A study on cellulase production from a mixture of lignocellulosic wastes. Process Biochem 83:148–158. https://doi.org/10.1016/j.procbio.2019.05.006
63. Ang SK, Shaza EM, Adibah Y, Suraini AA, Madihah MS (2013) Production of cellulases and xylanase by *Aspergillus fumigatus* SK1 using untreated oil palm trunk through solid state fermentation. Process Biochem 48(9):1293–1302. https://doi.org/10.1016/j.procbio.2013.06.019
64. De Castro RJS, Sato HH (2015) Enzyme production by solid state fermentation: general aspects and an analysis of the physicochemical characteristics of substrates for agro-industrial wastes valorization. Waste Biomass Valoriz 6:1085–1093. https://doi.org/10.1007/s12649-015-9396-x
65. Hansen GH, Lübeck M, Frisvad JC, Lübeck PS, Andersen B (2015) Production of cellulolytic enzymes from ascomycetes: comparison of solid state and submerged fermentation. Process Biochem 50(9):1327–1341. https://doi.org/10.1016/j.procbio.2015.05.017
66. Nascimento RP, Coelho RRR, Marques S, Alves L, Gırio FM, Bon EPS, Amaral-Collaço MT (2002) Production and partial characterisation of xylanase from *Streptomyces* sp. strain AMT-3 isolated from Brazilian cerrado soil. Enzyme Microb Technol 31:549–555. https://doi.org/10.1016/S0141-0229(02)00150-3
67. Kumar A, Gupta R, Shrivastava B, Khasa YP, Kuhad RC (2012) Xylanase production from an alkalophilic actinomycete isolate *Streptomyces* sp. RCK-2010, its characterization and application in saccharification of second generation biomass. J Mol Catal B 74:170–177. https://doi.org/10.1016/j.molcatb.2011.10.001
68. Ting ASY, Hermanto A, Peh KL (2014) Indigenous actinomycetes from empty fruit bunch compost of oil palm: evaluation on enzymatic and antagonistic properties. Biocatal Agric Biotechnol 3(4):310–315. https://doi.org/10.1016/j.bcab.2014.03.004
69. Zhang D, Luo Y, Chu S, Zhi Y, Wang B, Zhou P (2016) Enhancement of cellulase and xylanase production using pH-shift and dissolved oxygen control strategy with *Streptomyces griseorubens* JSD-1. Appl Biochem Biotechnol 178:338–352. https://doi.org/10.1007/s12010-015-1875-9
70. De Sales AN, de Souza AC, Moutta RDO, Ferreira-Leitão VS, Schwan RF, Dias DR (2017) Use of lignocellulose biomass for endoxylanase production by *Streptomyces termitum*. Prep Biochem Biotechnol 47(5):505–512. https://doi.org/10.1080/10826068.2016.1275015
71. Srivastava KC (1993) Properties of thermostable hemicellulolytic enzymes from *Thermomonospora* strain 29 grown in solid state fermentation on coffee processing solid waste. Biotechnol Adv 11(3):441–465. https://doi.org/10.1016/0734-9750(93)90013-D
72. Beg QK, Bhushan B, Kapoor M, Hoondal GS (2000) Enhanced production of a thermostable xylanase from *Streptomyces* sp. QG-11-3 and its application in biobleaching of eucalyptus kraft pulp. Enzyme Microb Technol 27:459–466. https://doi.org/10.1016/S0141-0229(00)00231-3
73. Bajaj BK, Singh NP (2010) Production of xylanase from an alkalitolerant *Streptomyces* sp. 7b under solid-state fermentation, its purification, and characterization. Appl Biochem Biotechnol 162:1804–1818. https://doi.org/10.1007/s12010-010-8960-x
74. Singh R, Kapoor V, Kumar V (2012) Utilization of agro-industrial wastes for the simultaneous production of amylase and xylanase by thermophilic actinomycetes. Braz J Microbiol 43(4):1545–1552. https://doi.org/10.1590/S1517-83822012000400039
75. Vivek N, Nair LM, Mohan B, Nair SC, Sindhu R, Pandey A, Shurpali N, Binod P (2019) Bio-butanol production from rice straw-Recent trends, possibilities, and challenges. Bioresour Technol Rep. https://doi.org/10.1016/j.biteb.2019.100224
76. Dixit PP, Deshmukh AM (2016) Xylanase from *Streptomyces hygroscopicus* under solid state fermentation. Int J Adv Biotechnol Res 7(1):38–46
77. Zhang F, Zhu Z, Wang B, Wang P, Yu G, Wu M, Chen W, Ran W, Shen Q (2013) Optimization of *Trichoderma harzianum* T-E5 biomass and determining the degradation sequence of biopolymers by FTIR in solid-state fermentation. Ind Crop Prod 49:619–627. https://doi.org/10.1016/j.indcrop.2013.05.037
78. Badhan A, Ribeiro GO Jr, Jones DR, Wang Y, Abbott DW, Di Falco M, Tsang A, McAllister TA (2018) Identification of novel enzymes to enhance the ruminal digestion of barley straw. Biores Technol 260:76–84. https://doi.org/10.1016/j.biortech.2018.03.086
79. Ishaque M, Kluepfel D (1981) Production of xylanolytic enzymes by *Streptomyces flavogriseus*. Biotechnol Lett 3(9):481–486. https://doi.org/10.1007/BF00147558
80. Mackenzie CR, Bilous D, Johnson KG (1984) Purification and characterization of an exoglucanase from *Streptomyces flavogriseus*. Can J Microbiol 30:1171–1178. https://doi.org/10.1139/m84-183
81. Chen WP, Anderson AW, Han YW (1979) Extraction of glucose isomerase from *Streptomyces flavogriseus*. Appl Environ Microbiol 37(4):785–787
82. Kluepfel D, Biron L, Ishaque M (1980) Simultaneous production of cellulose complex and glucose isomerase by *Streptomyces flavogriseus*. Biotechnol Lett 2(7):309–314. https://doi.org/10.1007/BF00172643
83. Srivastava R, Ali SS, Srivastava BS (1991) Cloning of xylanase gene of *Streptomyces flavogriseus* in *Escherichia coli* and bacteriophage λ-induced lysis for the release of cloned enzyme. FEMS Microbial Lett 78(2–3):201–206. https://doi.org/10.1111/j.1574-6968.1991.tb04443.x
84. Pennacchio A, Ventorino V, Cimini D, Pepe O, Schiraldi C, Inverso M, Faraco V (2018) Isolation of new cellulase and xylanase producing strains and application to lignocellulosic biomasses hydrolysis and succinic acid production. Bioresour Technol 259:325–333. https://doi.org/10.1016/j.biortech.2018.03.027
85. Chu FJ, Lin CW, Yet-Po I, Wu CH, Chen DH (2012) Hydrolysis of bamboo cellulose and cellulase characteristics by *Streptomyces griseoaurantiacus* ZQBC691. J Taiwan Inst Chem Eng 43(2):220–225. https://doi.org/10.1016/j.jtice.2011.08.004
86. Kumar AK (2015) UV mutagenesis treatment for improved production of endoglucanase and β-glucosidase from newly isolated thermotolerant actinomycetes *Streptomyces griseoaurantiacus*. Bioresour Bioprocess 2(1):22. https://doi.org/10.1186/s40643-015-0052-x
87. Iizuka H, Kawaminami T (1969) Studies on xylanase from microorganisms. Agric Biol Chem 33(9):1257–1263. https://doi.org/10.1080/00021369.1969.10859468
88. Macagnan D, Romeiro RDS, Pomella AWV, de Souza JT (2008) Production of lytic enzymes and siderophores, and inhibition of germination of basidiospores of *Moniliophthora* (ex Crinipellis) *perniciosa* by phylloplane actinomycetes. Biol Control 47:309–314. https://doi.org/10.1016/j.biocontrol.2008.08
89. Anzai Y, Watanabe J (1997) 16S rRNA gene sequence analysis of *Streptomyces lavendulae* and *Streptomyces virginiae* strains. Actinomycetologica 11(1):15–19. https://doi.org/10.3209/saj.11_15

90. Long K, Lu Z, Wu S, Peng L (2012) Screening and identification of an actinomycete antagonistic to pepper bacterial wilt. J Henan Agric Sci 41(11):92–95
91. Petricková K, Chronáková A, Zelenka T, Chrudimský T, Pospísil S, Petrícek M, Kristufek V (2015) Evolution of cyclizing 5-aminolevulinate synthases in the biosynthesis of actinomycete secondary metabolites: outcomes for genetic screening techniques. Front Microbiol 6:814. https://doi.org/10.3389/fmicb.2015.00814
92. Dezfully NK, Ramanayaka JG (2015) Isolation, identification and evaluation of antimicrobial activity of *Streptomyces flavogriseus*, strain ACTK2 from soil sample of Kodagu, Karnataka State (India). Jundishapur J Microbiol 8(2):e15107.7
93. Yang N, Sun C (2016) The inhibition and resistance mechanisms of actinonin, isolated from marine *Streptomyces* sp. NHF165, against Vibrio anguillarum. Front Microbiol 7:1467. https://doi.org/10.3389/fmicb.2016.01467
94. Yu J, Zhang L, Liu Q, Qi X, Ji Y, Kim BS (2015) Isolation and characterization of actinobacteria from Yalujiang coastal wetland, North China. Asian Pac J Trop Biomed 5(7):555–560. https://doi.org/10.1016/j.apjtb.2015.04.007
95. ShanW ZhouY, Liu H, Yu X (2018) Horticultural biology and metabolomics center, Haixia Institute of Science and Technology. Fujian Agriculture and Forestry University, China

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.