Draft genome sequences of two Streptomyces albidoflavus strains DEF1AK and DEF147AK with plant growth-promoting and biocontrol potential

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Abstract

Purpose: Bacteria belonging to the Streptomyces genus can be exploited in environmentally friendly approaches to food safety. Genome information can help to characterize bioactive strains opening the possibility to decipher their mechanisms of action.

Methods: The biocontrol and plant growth-promoting activity of two Streptomyces spp. strains, DEF1AK and DEF147AK, were assessed in vitro and in planta. The genome sequences were determined using the Illumina NextSeq sequencing system and were assembled using EvoCAT (Evogene Clustering and Assembly Toolbox).

Result: Streptomyces spp. DEF1AK and DEF147AK were able to improve seed germination and early plant development of maize, wheat, and tomato and inhibited the mycelium growth of diverse fungal plant pathogens in vitro. The genome sequence analysis identified both strains as S. albidoflavus (99% sequence identity). Both genomes were of 7.1-Mb length with an average GC content of 73.45%. AntiSMASH and MIBiG analyses revealed strain-specific sets of secondary metabolite gene clusters in the two strains as well as differences in the number and type of duplicated genes.

Conclusion: The combination of the biological activity and genomic data is the basis for in-depth studies aimed at the identification of secondary metabolites involved in plant growth-promoting and biocontrol activity of Streptomyces spp. The comparison of unique genomic features of the two strains will help to explain their diverse biocontrol and plant growth-promoting activities and warrant targeted functional genomics approaches to verify their mechanisms of action.

Keywords: Antagonism, Biological control, Genome mining, Secondary metabolites

Background

Streptomyces spp. are Gram-positive filamentous bacteria ubiquitous in the soil as free-living organisms and symbionts of plants and animals (Seipke et al. 2012). They are renowned for producing a wide variety of biologically active secondary metabolites, and therefore, there are increasing attempts to apply them in agriculture as plant growth promoters or biological control agents (BCA) (Xiao et al. 2002; Bonaldi et al. 2014; Colombo et al. 2019b, a; Liu et al. 2019). While until 2010, less than 10 reports were published yearly with the keywords ‘Streptomyces’ and ‘biocontrol’, in the last 10 years, 50–80 scientific papers have been published each year (www.scopus.com). This indicates increasing interest in the research for alternative methods to manage plant diseases.

Despite a large number of potentially active strains with good antagonistic activity against a variety of plant pathogens, only two Streptomyces-based products have
been registered so far for use in agriculture, based on *S. lydicus* WYEC 108 (Actinovate®) and *S. griseoviridis* K61 (Mycostop®). Among the main problems hindering the successful use of new BCAs is their variable performance in field conditions (Velivelli et al. 2014; Chen et al. 2016), possibly also due to the variable expression and production of bioactive molecules.

The expression of many bioactive molecules might be silenced in sub-optimal growth conditions, or on the other side, specifically activated by the presence of a specific elicitor (Wang et al. 2013). In *Streptomyces*, genes for the biosynthesis of secondary metabolites are mostly clustered and their expression is tightly regulated (Čihák et al. 2017). The genome analysis of bioactive strains can provide information about the secondary metabolite composition and can help understanding how the expression of these bioactive molecules is regulated (Lee et al. 2020).

In order to get a holistic view on the bioactive potential of two *Streptomyces* spp., DEF1AK and DEF147AK, their biocontrol and plant growth promotion activity were assessed and the draft genome sequences were obtained to identify secondary metabolite clusters possibly responsible for the biocontrol activity.

**Results**

**Biocontrol potential of *Streptomyces* spp. in vitro and in planta**

Both *Streptomyces* spp. DEF1AK and DEF147AK showed a significant ability to limit fungal growth of different fungal genera in dual culture assay (Fig. 1); however, DEF147AK showed consistently higher biocontrol activity in vitro.

The two strains were effective also when associated with the plant (Table 1, Fig. 2). Surprisingly, in association with wheat seedlings, DEF1AK was able to reduce the symptoms of both *Fusarium* root rot and *Fusarium* foot rot to a higher extent than DEF147, even though it showed lower in vitro inhibition of *Fusarium* pathogens. In particular, 45% of DEF1AK-treated plants were symptomless at the crown level, while only 5% of control plants did not show any symptoms.

**Effect of *Streptomyces* spp. on seed germination and biomass dry weight in vivo**

The plant growth-promoting potential of *Streptomyces* spp. DEF1AK and DEF147AK was tested by evaluating their effect on seed germination of various mono- and dicotyledonous plants (Fig. 3) and on the biomass accumulation after 1 month of cultivation (Table 2). DEF1AK in general did not influence the seed germination of tested species, only in the case of savoy cabbage it increased the seed germination by almost 10%, while it had a negative impact on lamb lettuce germination (25% decrease in germination). On the other hand, DEF147AK improved the germination of monocotyledonous plants (10% increase in maize and wheat), while it generally had a negative impact on the dicotyledonous plant germination, except tomato (no change) and rocket (8% increase).

After 1 month of growth, DEF1AK only slightly improved the biomass dry weight of maize and tomato (not statistically significant). DEF147AK instead significantly improved the biomass dry weight of maize, tomato, rocket, and lettuce (Table 2).
Draft genome analysis of *Streptomyces* spp. DEF1AK and DEF147AK

The sequencing and assembly statistics for the two strains are listed in Table 3.

Phylogenetic strain attribution was carried out using a *Streptomyces* multilocus sequence type (MLST) analysis (Jolley and Maiden 2010), and the closest related type strain to both DEF1AK and DEF147AK was *Streptomyces albidoflavus* DSM 40455 T. Indeed, MLST analysis is the most appropriate method for correct identification of closely related *Streptomyces* species belonging to the *S. albidoflavus* clade, which share the same 16S rDNA sequence (Hain et al. 1997; Guo et al. 2008). The average nucleotide identity (ANI) implemented in EZBioCloud (Yoon et al. 2017) determined ANI equal to 99.04% and 99.06% by comparing *S. albidoflavus* DSM 40455 T to DEF1AK and DEF147AK, respectively. By comparing DEF1AK and DEF147AK genomes, ANI = 99.91% was obtained, suggesting that the two strains belong to the same species.

Both genomes contained more than 6000 CDS, and among these, 83% were classified into 23 clusters of orthologous proteins, such as transcription, amino acid transport and metabolism, carbohydrate transport and metabolism, and signal transduction (Huerta-Cepas et al. 2016, 2017). Almost 30% of genes were poorly characterized with unknown function (Supplementary file 1). The similarity comparison with the PkGDB Synteny statistics (Vallenet et al. 2019) revealed that 6534 (98.21%) CDS are organized in a single conserved block (synteny) between DEF1AK and DEF147AK.

AntiSMASH (v5.0.0) and MIBiG (v4.1) analysis predicted a total of 29 and 33 secondary metabolite biosynthetic clusters in DEF1AK and DEF147AK, respectively (Blin et al. 2019). To get a better insight into the prevalence of different secondary metabolite clusters within the *S. albidoflavus* clades, the AntiSMASH analysis was performed also for the type strain *S. albidoflavus* DSM 40455 T, a recently sequenced *S. albidoflavus* ACT 77 (Pylro et al. 2019), and *S. albidoflavus* SM 254, whose complete genome sequence is available (Badalamenti et al. 2016). Both DEF1AK and DEF147AK strains encoded complete gene clusters for the synthesis of well-known terpene geosmin responsible for the typical earth-like smell common for streptomycetes, a siderophore desferrioxamine B, or stress-protectant osmolyte ectoine. There were multiple gene clusters encoding type-a polyketide synthases (t1pks) and non-ribosomal peptides (NRP)—the most common enzymes responsible for the biosynthesis of a variety of secondary metabolites. They showed a different level of homology to clusters coding for known antifungal and antibacterial molecules (Supplementary file 2) suggesting their putative role as biocontrol and plant interaction molecules (Vesselinova et al. 1991; Li et al. 2015; Chevrette et al. 2019).

**Table 1** Protection indices (%) of *Streptomyces* spp. DEF1AK and DEF147AK against *Fusarium* root rot (browning extension and browning index) and *Fusarium* foot rot (crown necrosis) symptoms caused by *Fusarium graminearum* Fg 8/1, on wheat seedlings (*Triticum aestivum* ‘Bandera’).

|                         | DEF1AK   | DEF147AK |
|-------------------------|----------|----------|
| Reduction of browning extension (4dai) | 17.60%   | 0.00%    |
| Reduction in browning index (6dai)     | 49.56%   | 18.39%   |
| Reduction of crown necrosis (6dai)     | 57.02%   | 31.74%   |

dai = days after pathogen inoculation

![Fig. 2 Effect of *Streptomyces* spp. DEF1AK (black) and DEF147AK (grey) treatment on *Fusarium* foot rot (FFR) symptoms severity caused by *Fusarium graminearum* Fg 8/1, on wheat seedlings (*Triticum aestivum* ‘Bandera’) 6 days after fungus inoculation. Scale used in FFR severity evaluation at the crown level: 0 = symptomless; 1 = slightly necrotic; 2 = moderately necrotic; 3 = severely necrotic; 4 = completely necrotic (Colombo et al. 2019b).](image-url)
Although all analysed strains encode biosynthetic pathways for the production of cyclic depsipeptides or lanthipeptides, there seem to be differences in the final secondary metabolite produced (antimycin or candicidin, AmfS or SapB). We hypothesize that the combination of particular secondary metabolites produced by a specific strain can, in the end, result in different plant growth-promoting or biocontrol activity. Given the influence of the genome completeness on the output of AntiSMASH analysis, the actual production of these secondary metabolites will be investigated in the future.

Conclusions

The *Streptomyces* genus is an enormous reservoir of bioactive molecules exploited mainly in medicine and, until now, only to a minimal extent in agriculture. However, their ubiquitous presence in soils and their association with plants as epiphytes or endophytes makes them an ideal resource for improving plant productivity and health (Seipke et al. 2012; Jauri et al. 2016).

In this paper, we analysed two *Streptomyces* spp. strains identified as *S. albidoaflavus* based on genomic data, with 99.91% average nucleotide identity between

![Table 2](image_url)

| Dry weight (g)     | Control | DEF1AK | DEF147AK | No. plants | P value* |
|--------------------|---------|--------|----------|------------|----------|
| Maize (10 dai)     | 0.63 ± 0.06 b^b^ | 0.69 ± 0.06 ab | 0.83 ± 0.04 a | 20 | 0.0263 |
| Rice 'Carnaroli' (14 dai) | 0.14 ± 0.05 ns | 0.14 ± 0.04 ns | 0.15 ± 0.04 ns | 20 | 0.553 |
| Wheat 'Banderina' (3 dai) | 0.25 ± 0.03 b | 0.28 ± 0.04 ab | 0.30 ± 0.07 a | 20 | 0.0124 |
| Tomato 'Marramone' (6 dai) | 0.12 ± 0.02 b | 0.12 ± 0.02 b | 0.18 ± 0.03 a | 20 | 1.11 × 10^{-11} |
| Rocket (10 dai)    | 0.12 ± 0.04 ns | 0.09 ± 0.03 ns | 0.08 ± 0.05 ns | 20 | 0.0977 |
| Savoy cabbage 'Piacentino' (10 dai) | 0.16 ± 0.04 ns | 0.17 ± 0.04 ns | 0.14 ± 0.05 ns | 10* | 0.0971 |
| Cauliflower (7 dai) | 0.35 ± 0.08 ns | 0.34 ± 0.06 ns | 0.30 ± 0.06 ns | 20 | 0.0655 |
| Lettuce (10 dai)   | 0.16 ± 0.04 b | 0.13 ± 0.03 b | 0.21 ± 0.04 a | 20 | 9.21 × 10^{-7} |
| Lamb lettuce       | 0.07 ± 0.02 ab | 0.07 ± 0.02 b | 0.09 ± 0.03 a | 20 | 0.0288 |

*Due to low germination of savory cabbage seeds, only 10 plants per treatment were analysed

*The mean value followed by the standard deviation

*Tukey post hoc test; mean values in the same row with the same letters are not significantly different (P = 0.05); ns not significant

*P value of the ANOVA analysis
them. Despite such a high similarity, the two strains showed clearly different plant growth and biocontrol potential. While DEF147AK inhibited a variety of fungal plant pathogens to a higher extent in vitro and showed high variability in promotion or inhibition of plant growth, DEF1AK proved to control better the Fusarium foot and root rot in planta. The ability to have higher activity in planta can be partially explained by the analyses of duplicate tandem genes (Supplementary file 3) which indicate potential selective pressure to maintain functional redundancy (Bratlie et al. 2010; Kondrashov 2012). Indeed, DEF1AK has a larger number of duplicated genes, such as ABC transporters, which can partially explain its better fitness in planta conditions. Both strains presented a set of duplicated chitinases that can act as effectors in the limitation of fungal growth in vitro. Moreover, Palazzini et al. (2017, 2018) demonstrated the activity of S. albidoflavus RC 87B against pathogenic Fusarium graminearum and deoxynivalenol (DON) accumulation in field conditions. Their results together with the DEF1AK activity in planta indicate the presence of specific secondary metabolites within the S. albidoflavus cluster able to counteract Fusarium species and DON accumulation.

Based on the genomic data, both strains have the potential to produce a variety of secondary metabolites, documented by the presence of 29 and 33 biosynthetic clusters in DEF1AK and DEF147AK, respectively. The differences in the secondary metabolite arsenal may explain the different biocontrol and PGP potential of the two strains.

Overall, our comparative report integrating biological activity with genomic data of two biologically active Streptomyces strains can open the way towards the effective exploitation of these strains as PGP and biological control agents, deciphering the functional determinants of the bioactive characters (Malik et al. 2020). Further studies will determine if the subtle differences in the two genomes are responsible for the differential synthesis of biologically active compounds and if these are responsible for the differences in the biocontrol and plant growth promotion activity of the two strains.

Materials and methods

Streptomyces strains

The two Streptomyces spp. strains, DEF1AK and DEF147AK, used in this work are part of a wide actinomycete collection isolated from roots of various plants and conserved in the laboratory of Plant Pathology, at the Department of Food, Environmental and Nutritional Sciences (DeFENS), University of Milan, Italy (Sardi et al. 1992). DEF1AK was isolated from the root cortical layer of Amaryllis belladonna and DEF147AK from the root cortical layer of Betula pendula. Strains were grown on Czapek-Yeast Extract medium (CZY: 35 g/L Czapek Dox broth, Difco Laboratories, Detroit, MI, USA; 2 g/L yeast extract, Difco Laboratories, Detroit, MI, USA; 15 g/L agar, Applichem, Darmstadt, Germany) for 3 weeks at 24 °C. Spores were collected in 10% sterile glycerol (ICN Biomedicals, Irvine, CA, USA) + 0.01% tween 20 (Sigma-Aldrich, St. Louis, MO, USA) and filtered through two layers of sterile gauze. The concentration was determined by plating serial dilutions of spore suspension and calculating the CFU/ml, and the spore suspension was stored at –20 °C.

Fungal plant pathogens

Botrytis cinerea BC-2F-2016, BC-3F-2016, and BC-4F-2016; Fusarium graminearum PH1 (Cuomo et al. 2007), NRRL 28336 (Pasquali et al. 2016), 453 (Pasquali et al. 2013a), Fg8/1 (Boenisch and Schäfer 2011), and CS3005 (Gardiner et al. 2014); F. culmorum FcUK (Pasquali et al. 2013b); Sclerotinia sclerotiorum FW361, SSP2, and SSV1; and Pythium ultimum FW407 belong to a collection maintained in the laboratory of Plant Pathology at DeFENS, University of Milan, Italy. Rhizoctonia solani FW408 was kindly provided by Dr. Andrea Minuto (Centro di Sperimentazione e Assistenza Agricola, Albenga, Italy). The pathogens were maintained on Malt-Extract Agar medium (MEA: 30 g/L malt extract, Difco Laboratories, Detroit, MI, USA; 15 g/L agar, Applichem, Darmstadt, Germany) at 20 °C.

Dual culture assay in vitro

The biological activity of the two Streptomyces strains was evaluated as described in Kunova et al. 2016. Briefly, the pathogen agar-mycelium disc (6-mm diameter), taken from the edge of an actively growing fungal colony, was inoculated upside down in the centre of the Petri plate containing CZY, whereas 10 μL of streptomycete agar-spore suspension (10⁷ CFU/ml) were uniformly distributed along a 40-mm line. The inoculation distance between the pathogen and the Streptomyces strain, the day of pathogen inoculation, and the day of the measurement varied based on the growth rate of the pathogen (Table 4).

### Table 3 Draft genome sequencing and assembly statistics of Streptomyces spp. DEF1AK and DEF147AK

| Strain          | Total reads | Mean coverage (X) | No. scaffolds | N50 (bp) | Assembly length (bp) | G+C content (%) | Total No. genes | Avg. CDS length (bp) | No. rRNAs | No. tRNAs |
|-----------------|-------------|-------------------|---------------|----------|----------------------|----------------|-----------------|----------------------|-----------|-----------|
| DEF1AK          | 1,155,828   | 48x               | 131           | 107,416  | 7,095,674            | 73.46          | 6646            | 968                  | 4         | 65        |
| DEF147AK        | 1,272,519   | 50x               | 125           | 119,828  | 7,097,259            | 73.45          | 6620            | 978                  | 4         | 69        |
Three replicates were prepared for each strain, and plates inoculated only with the pathogen were used as control. Following the inoculation, plates were incubated in dark at 24 °C. The antagonistic activity was expressed as the percentage of mycelium growth inhibition compared to the control. It was calculated by the formula: (R1−R2)/R1 × 100, where R1 was the radius measurement from the centre of the fungal colony towards the edge in the control and R2 was the radius from the centre towards the edge of the fungal colony in the direction of the antagonist, respectively.

Effect of Streptomyces spp. on seed germination in vivo
Seeds of monocotyledonous plants maize (Zea mays L.), rice (Oryza sativa L., ‘Carnaroli’), and wheat (Triticum aestivum L., ‘Bandera’), and dicotyledonous plants tomato (Solanum lycopersicum L., ‘Marmande’), cultivated rocket (Eruta sativa Mill.), savoy cabbage (Brassica oleracea L., ‘Piacentino’), cauliflower (Brassica oleracea L., ‘Violetto di Sicilia’), soybean (Glycine max (L.) Merr.), lettuce (Lactuca sativa L., ‘Bionda ricciolina’), and lamb lettuce (Valerianella locusta L., ‘Accent’) were surface sterilized in 0.7% sodium hypochlorite for 5–10 min and rinsed three times abundantly in sterile water. Subsequently, they were bacterized by immersion of the seeds in a sufficient amount of Streptomyces spore suspension (10^7 CFU/mL) and letting them air-dry under the laminar flow hood. Control seeds were treated with sterile water. The seeds were sown in polystyrene seed trays (84 cells—48 cm^3 each) in the non-sterilized Irish and Baltic peat-based growing substrate (Vigorplant, Italy) in plastic boxes (10 × 10 × 10 cm) or polystyrene seed trays (84 cells—48 cm^3 each). The plants were grown in the growth chamber at 24 °C, 55% relative humidity, and a 15-h photoperiod and watered as necessary with tap water to keep the soil moist. After 1 month of growth (25 days in the case of wheat seedlings), the plants were carefully removed from the boxes, and the growing substrate was carefully removed from roots. Twenty plantlets per treatment were counted (ten plants for the savoy cabbage), left to air-dry at room temperature, and the biomass dry weight was determined.

Biocontrol potential of the two Streptomyces spp. strains against Fusarium graminearum on wheat seedlings
The biocontrol potential of the Streptomyces spp. strains against Fusarium root rot (FRR) and foot rot (FFR) was evaluated using F. graminearum Fg8/1-infected seedlings, as described in Colombo et al. (2019a). In detail, seeds of Triticum aestivum L. ‘Bandera’ were surface-sterilized in 0.7% sodium hypochlorite for 5 min and rinsed 3 times in sterile water. In sterile Petri dishes, seeds (N = 20) were inoculated with 1 mL of Streptomyces strain spore suspension (10^7 spores/mL) and dried under the laminar flow hood. Control seeds were treated with 1 mL of deionized sterile water. The assay took place in sterile glass dishes as seed trays (diameter 150 mm). In each dish, a filter paper was placed and soaked with 10-mL deionized sterile water before sowing. The dishes were placed at 5 °C in the dark for 24 h simulating a period of vernalization and then moved at 20 °C in the dark. Seventy-two hours after seed bacterization, dishes were placed in a growth chamber (21 °C, 16-h photoperiod using fluora lamp Osram L36W/77). Seedlings were watered with sterile deionized water every 2 days. Four days after seed bacterization, the seedlings were inoculated with an agar-mycelium plug (6-mm diameter) taken from the edge of an actively growing F. graminearum Fg8/1 colony and inoculated upside down on the roots at a 10-mm distance from the seed.

Effect of Streptomyces spp. on plant biomass in vivo
Seeds of diverse plant species were bacterized by the two Streptomyces spp. strains as described above and sown in the non-sterilized Irish and Baltic peat-based growing substrate (Vigorplant, Italy) in plastic boxes (10 × 10 × 10 cm) or polystyrene seed trays (84 cells—48 cm^3 each). The plants were grown in the growth chamber at 24 °C, 55% relative humidity, and a 15-h photoperiod and watered as necessary with tap water to keep the soil moist. After 1 month of growth (25 days in the case of wheat seedlings), the plants were carefully removed from the boxes, and the growing substrate was carefully removed from roots. Twenty plantlets per treatment were counted (ten plants for the savoy cabbage), left to air-dry at room temperature, and the biomass dry weight was determined.

Table 4 Parameters of the in vitro antibiosis assay

| Fungal plant pathogen | Inoculation distance | Streptomyces inoculation | Fungus inoculation | Measurement |
|-----------------------|----------------------|-------------------------|-------------------|------------|
| Botrytis cinerea BC-2F-2016, BC-3F-2016, BC-4F-2016 | 2.0 cm | Day 1 | Day 3 | Day 6 |
| Fusarium graminearum PHI, 453, NRRL 28336 | 2.5 cm | Day 1 | Day 3 | Day 5 |
| Fusarium graminearum CS3005 | 2.0 cm | Day 1 | Day 1 | Day 4 |
| Fusarium culmorum FcUK | 2.0 cm | Day 1 | Day 3 | Day 5 |
| Pythium ultimum FW407 | 2.5 cm | Day 1 | Day 1 | Day 4 |
| Rhizoctonia solani FW408 | 2.0 cm | Day 1 | Day 1 | Day 4 |
| Sclerotinia sclerotiorum FW361, SSP2, SSV1 | 2.5 cm | Day 1 | Day 3 | Day 5 |

The distance of inoculation between the Streptomyces and fungal plant pathogen, the timing of Streptomyces and fungal plant pathogen inoculation, and the timing of the fungal radial growth measurement.
Four days after pathogen inoculation FRR was measured on 20 roots as necrosis development. FRR data were reported as millimetres of necrosis extension. Percentages of necrosis inhibition (NI%) were calculated by comparing measurements of necrosis on the control (N<sub>C</sub>) and the treated seedlings (N<sub>T</sub>) using the equation: NI% = (N<sub>C</sub> − N<sub>T</sub>)/N<sub>C</sub> × 100.

Six days after pathogen inoculation, FFR was evaluated by scoring the symptoms at the crown level on 20 seedlings (Covarelli et al. 2013) with a 0–4 scale (0 = symptomless; 1 = slightly necrotic; 2 = moderately necrotic; 3 = severely necrotic; 4 = completely necrotic). The FFR disease severity index (DSI) was calculated for each treatment using the equation: DSI = (disease grade x number of plants in each grade)/(total number of plants x the highest disease grade) x 100. The ability of *Streptomycyes* spp. strains to reduce FFR symptoms was calculated as protection percentage (P%) which was calculated using the equation: P% = (DSI<sub>C</sub> − DSI<sub>T</sub>)/DSI<sub>C</sub> x 100, where DSI<sub>C</sub> and DSI<sub>T</sub> were the DSI in control and treated seedlings, respectively.

**DNA extraction and genome sequencing**

To obtain the DNA for the genome sequencing, the spore suspensions were inoculated in a Czapek Yeast Extract liquid medium (35 g/L Czapek dox broth, Difco Laboratories, USA, 2 g/L yeast extract, Difco Laboratories, USA) and grown for 7 days at 25 °C with a 100 rpm constant orbital shaking. The mycelium and spores were collected by centrifugation and the DNA was extracted and purified using the CTAB procedure for the isolation of genomic DNA (Kieser et al. 2000). The total DNA was randomly fragmented by sonication and the sequencing library was prepared using the Kapa HyperPrep Kit (Roche, Switzerland). Sequencing was carried out using the Illumina NextSeq 500/550 Mid Output v2 Kit (Illumina Inc., USA) on Illumina NextSeq 500 system. The draft genomes were assembled using EvoCAT (Evogene Clustering and Assembly Toolbox), which is a part of Evogene’s computational biology predictive (CPB) platform (https://www.evogene.com) and annotated using MicroScope platform (Vallenet et al. 2019).

**Additional file 1: Table S1.** Clustering of *Streptomycyes* spp. DEF1AK and DEF147AK CDS based on the EggNOG orthology (Huerta-Cepas et al. 2016; Vallenet et al. 2019).

**Additional file 2: Table S2.** Secondary metabolite analysis of *Streptomycyes albidoflavus* DSM 40455<sup>T</sup>, ACT777, SM 254, DEF1AK and DEF147AK by AntiSMASH based on homology to genome clusters from the database (Blin et al. 2019; Kautsar et al. 2020).

**Additional file 3: Table S3.** List of genomic regions containing tandem duplications of protein coding genes. Tandem duplicated genes have an identity ≥35% with a minLRap 2018 and are separated by a maximum of 5 consecutive genes. Begin: starting position of the genomic region; End: end position of the genomic region; Gene number: number of tandem duplicated genes contained in the genomic region; Genes: description of the tandem duplicated genes with their label, gene name and product description (Vallenet et al. 2019).
induction by two selected antagonists. Toxins (Basel) 10:1088 https://doi.org/10.3390/toxins10020088
Palazzini JM, Yerkovich N, Alberiome E, et al (2017) An integrated dual strategy to control Fusarium graminearum sensu stricto by the biocontrol agent Streptomyces sp. RC 878 under field conditions. Plant Gene 9:13–18. https://doi.org/10.1016/j.plgene.2016.11.005
Pasquali M, Cocco E, Guignard C, Hoffmann L (2016) The effect of agonate on trichothecene type B and zearealene production in Fusarium graminearum, F. culmorum and F. poae. PeerJ 2016:e1672. https://doi.org/10.7717/peerj.1672
Pasquali M, Serchi T, Renaut J, et al (2013a) 2D difference gel electrophoresis reference map of a Fusarium graminearum nivalenol producing strain. Electrophoresis 34:505–509. https://doi.org/10.1007/s10689-012-2002-56
Pasquali M, Spanu F, Scherm B, et al (2013b) FcStuA from Fusarium culmorum controls wheat foot and root rot in a toxin dispensable manner. PLoS One 8:e57429. https://doi.org/10.1371/journal.pone.0057429
Pyro VS, Dias ACT, Andreote FD, et al (2019) Draft genomic sequences of Streptomyces misionensis ACT66 and Streptomyces albidoflavus ACT77, bacteria with potential application for phytopathogen biocontrol. Microbiol Resour Announc 8:949–968. https://doi.org/10.1128/mra.00949-19
Sardi P, Saracchi M, Quaroni S et al (1992) Idiation of endophytic Streptomyces strains from surface-sterilized roots. Appl Environ Microbiol 58:2691–2693
Seipke RF, Kaltenpoth M, Hutchings MI (2012) Streptomyces as symbionts: an emerging and widespread theme? FEMS Microbiol Rev 36:862–876. https://doi.org/10.1111/j.1574-696X.2011.00313.x
Vallenten D, Calteau A, Dubois M, et al (2019) MicroScope: an integrated platform for the annotation and exploration of microbial gene functions through genomic, pangenomic and metabolic comparative analysis. Nucleic Acids Res 47:541–549. https://doi.org/10.1093/nar/gkz026
Velivelli SSLS, De Vos P, Kromann P, et al (2014) Biological control agents: from field to market, problems, and challenges. Trends Biotechnol 32:493–496. https://doi.org/10.1016/j.tibtech.2014.07.002
Vesselinova N, Ghesheva R, Ivanova V (1991) Streptomyces species producing the streptovaricin complex. Folia Microbiol (Praha) 36:538–541. https://doi.org/10.1007/s10482-017-0844-4
Wang D, Yuan J, Gu S, Shi Q (2013) Influence of fungal elicitors on biosynthesis of natamycin by Streptomyces natalensis HW-2. Appl Microbiol Biotechnol 97:5527–5534. https://doi.org/10.1007/s00253-013-4786-0
Xiao K, Kinkel LL, Samac D a. (2002) Biological control of Phytophthora root rot on alfalfa and soybean by Streptomyces. Biol Control 23:285–295. https://doi.org/10.1006/bioc.2001.0175
Yoon SH, Ha S min, Lim J, et al (2017) A large-scale evaluation of algorithms to calculate average nucleotide identity. Antonie Van Leeuwenhoek 110:1281–1286. https://doi.org/10.1007/s10482-017-0844-4

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